UNIVERSITY OF ALBERTA

Tropical Dry Forest Regeneration and its Influence on Three Species of Costa Rican Monkeys

by

Troy Christian Sorensen ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Tropical Dry Forest Regeneration And Its Influence On Three Species Of Costa Rican Monkeys submitted by Troy Christian Sorensen in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

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Abstract

TROPICAL DRY FOREST REGENERATION AND ITS INFLUENCE ON THREE SPECIES OF COSTA RICAN MONKEYS

Troy Christian Sorensen

Only 2% of tropical dry forest in Central America remains undisturbed; consequently habitat regeneration is the only option left to conserve adequate areas of habitat. I studied the influence of a forest regeneration gradient (0 - 130 years since abandonment) on the abundance and group composition of white-faced capuchins (*Cebus capucinus*), howling monkeys (*Alouatta palliata*), and spider monkeys (*Ateles geoffroyi*) in the tropical dry forest of Santa Rosa National Park, Costa Rica. Trees and monkey densities were sampled using 600m transects within each of 14 sites from February to June 1996. Tree species composition and structure showed consistent trends with forest age. Densities of all three monkey species increased as the forest regenerated. Monkey food biomass was estimated from the tree data and was highly correlated with densities of each monkey species. The results indicate that forest structure and species composition, monkey habitat, and consequently viable monkey populations, can be regained through protection and consequent natural regeneration of tropical dry forest.

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I. Introduction

The largest single component of the world's tropical forest is dry forest (42%, Holdridge 1967; Brown and Lugo 1982) yet dry forest has been relatively neglected in ecosystem research (Murphy and Lugo 1986a). In Pacific Central America, tropical dry forest is characterized by 900 to 2400 mm of annual rainfall and a severe dry season with no rain between Jan and April (Janzen 1986a). Unlike humid tropical forests, the species composition, stand structure, and biomass of dry tropical forest has been understudied (Murphy and Lugo 1986b).

At one time, a continuous strip of tropical dry forest covered much of the Pacific coast between Mexico and Panama, and constituted half of all Central American forests (Janzen 1986a; Murphy and Lugo 1986a). Currently less than 2% of the original area is in an undisturbed state and only 0.09% is protected (Janzen 1986a) which renders tropical dry forest as the most threatened of all lowland tropical forest types (Janzen 1988). In Central America, agriculture (cotton, sugar cane, banana, rice, beans, maize) and extensive cattle ranching have resulted in tropical dry forest existing only as fragments and degraded patches (Janzen 1986a). Deforestation increased in the 1950's due to the construction of the Inter-American highway (Tosi 1980; Sader and Joyce 1988) and by the 1970's, 4% of the tropical dry forest in Costa Rica was being deforested each year (Tosi 1980).

One method used to counteract the loss of forest is land restoration and subsequent habitat regeneration. Protection of the remaining intact patches would be insufficient to save the ecosystem; therefore knowledge of natural succession in tropical dry forest is crucial to reclaim disturbed land and to establish sustainable land use programs (Sabogal 1992; Gerhardt 1994; Janzen 1986a). By better understanding tropical dry forest regeneration, conservationists can develop sustainable management plans with specific goals for species composition and structure.

The abundance and distribution of many animal species have been severely altered due to the deforestation and fragmentation of tropical dry forest. Research on wildlife

populations such as monkeys in regenerating habitats can provide important information on their ability to utilize forests of different disturbance histories (Frumhoff 1995), and information on the habitat qualities that attract monkey groups. With such information, conservationists can better evaluate usable habitat and set goals for potential population sizes, and thus develop management strategies.

Tropical forest primates have been considered important indicator species of ecosystems for several reasons. Their relatively slow reproductive rates and rarity makes them more susceptible to disturbance and habitat changes (Bearder 1991; Fedigan et al. 1996). The influence of habitat can be compared between sympatric species with a wide range of diets and group compositions. They can compose a large portion of total herbivore biomass in tropical ecosystems (Terborgh 1986). Furthermore, arboreal species are influenced by forest structure and forest fragmentation. Lastly, primates tend to attract important public conservation interest (Bearder 1991; Fedigan et al. 1996). In addition to their suitability as indicators, primates have an intrinsic role in ecosystems as herbivores, as seed dispersal agents, and by pruning vegetation (Bourliere 1985; Bearder 1991). In theory, habitat disturbance could result in changes in population density, group density, group size, sex ratio, age structure, genetic diversity, and social interactions. However, primates in tropical dry forest are under-studied and much more quantitative research is needed to construct conservation and management plans (Chapman et al. 1989).

The abundance of abandoned pastures of various ages in Central America makes the study of regeneration possible with a cross-sectional approach, assuming that the original vegetation was similar for all study sites. Santa Rosa National Park (S.R.N.P.), Costa Rica, is a mosaic of various disturbance histories from centuries of human use and has great potential for static comparisons. In the mid 1520's the first conquistadors traveled through the northern region of Costa Rica and by the late 1500's 'Hacienda Santa Rosa' was established as a 700km^2 cattle ranch (Janzen 1986a). Over the following 400 years, Hacienda Santa Rosa was subdivided and sold to various owners. In May 1971, Santa Rosa was declared a National Park, and in 1977 the park was enlarged to include the

park's major drainage basins (Janzen 1986b). The history of S.R.N.P. has resulted in many forest patches of a wide range of ages and disturbance histories.

Three species of monkeys inhabit the park: white-faced capuchins (*Cebus capucinus*), mantled howling monkeys (*Alouatta palliata*), and red spider monkeys (*Ateles geoffroyi*). Populations of these species have been studied within the park since the 1970's and much of the background biology is now available including their overall numbers, diet, home ranges, group compositions, social behavior, and associations with generalized habitats.

Chapters 2 and 3 of this thesis deal with the two main objectives of this study. In chapter 2 I examine the structure and species composition of tropical dry forest along a regeneration gradient. Community level analyses of the tree species allow me to examine species diversity and rates of change in species composition through forest regeneration. I associate particular tree species with different stages of regeneration, and I analyze the change in forest structure, such as tree height and density, from pasture abandonment to forest maturity.

In chapter 3 I examine the influence of this forest regeneration gradient on three sympatric monkey species. At what age of regeneration does the forest contain suitable habitat to attract and sustain populations of these species? To answer this I examine the density, group size, and group composition of the three monkey species along a regeneration gradient from pasture abandonment to forest maturity.

In the concluding chapter I summarize the management and conservation implications of the two preceding chapters and suggest directions for future research on the regeneration of tropical dry forest and its monkeys.

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II. Tree Species Composition And Structure Of Tropical Dry Forest Along A Regeneration Gradient In Santa Rosa National Park, Costa Rica

INTRODUCTION

Tropical dry forest constitutes the largest proportion of tropical forests in the world (Brown and Lugo 1980, 1982), but is also the most endangered (Janzen 1988a, b). On the Pacific coast of Central America, less than 2% of dry forest is intact and only 0.09% is protected (Janzen 1986a, 1988a, b). Despite this, the structure and species composition of tropical dry forest is relatively understudied (Murphy and Lugo 1986a, b). Protection of the remaining intact patches would be insufficient to save the ecosystem; hence knowledge of natural succession in tropical dry forest is crucial to reclaim disturbed land and establish sustainable land use programs (Sabogal 1992; Gerhardt 1994; Janzen 1986a).

Longitudinal studies of the regeneration of tropical dry forests have been limited to examining forests during the first 3 years of regeneration (Ewel 1977; Opler et al. 1977), and attempts to infer forest regeneration from static comparisons are rare (Ewel 1971; Brown and Lugo 1990; Sabogal 1992). The abundance of abandoned pastures of various ages in Central America makes the study of regeneration possible with a static approach, assuming that the original vegetation was similar for all study sites.

Today's mature tropical forests are results of current and previous human and natural disturbances (Hartshorn 1980); therefore conservationists do not know what constitutes an 'original' or 'pristine' climax community (Lugo 1988). The silviculture and agricultural practices of indigenous peoples long before Spanish settlement (Hartshorn 1980; Gomez-Pompa et al. 1987; Gomez-Pompa 1991) may have influenced current views of climax communities and forest structure. We can only remove current anthropogenic disturbances and accept any stabilization after an arbitrary amount of time as representative of current climax vegetation.

Shugart and Hett (1973) found that changes in species composition (succession) decreased with time, suggesting the approach to a climax community. From anecdotal evidence, tropical dry forests are estimated to converge into a climax community and completely recover from disturbance at 100-150 years (Opler et al. 1977; Janzen 1986a). The time required for tropical dry forest to return to a mature state is empirically examined in this study by comparing the species composition of different aged forests. This approach also reveals species-specific associations with various stages of forest regeneration following pasture abandonment.

Conservationists have emphasized the protection of climax communities because these communities are believed to have the highest species diversity (Shugart and Hett 1973) and complex forest structure. To test these assumptions, the species diversity and structure of tropical dry forest will be examined along a regeneration gradient.

The characteristics of tree species will differ in each stage of succession (Budowski 1965; Oldeman and Van Dijk 1991). It is generally suggested that early successional species have high dispersal abilities and small seed size, while mature forest species have large, high quality seeds with competitive ability in saturated habitats (Howe and Smallwood 1982). Therefore, the proportion of trees with wind dispersed diaspores may decrease with succession (Budowski 1970; Janzen 1988a). The proportion of trees with compound and deciduous leaves has also been suggested to decrease through succession (Budowski 1970; Givnish 1978; Opler 1978, Janzen 1986a,b). Differences in these tree characteristics will be examined along a regeneration gradient. Tree species characteristics will also be discussed in light of their potential influence on wildlife.

METHODS

Study Site

Santa Rosa National Park is located (10° 50'N, 85° 39'W) 35 km northwest of Liberia, Guanacaste, Costa Rica. The park was established in 1971 and is now within the much larger (1,100 km^2) protected area of Area de Conservation Guanacaste. The park consists of 108 km^2 of tropical dry forest (Tropical Dry Forest and Premontane Moist Forest, Holdridge et al. 1971) covering an upper and lower plateau (300-0 m elevation). The

park receives 800-2600 mm of rainfall annually with temperatures ranging from 21.6 (Sept.) to 34.4 °C (April; Janzen in Gerhardt 1994). The park experiences a severe dry season from mid December to late May in which virtually no rain falls and deciduous trees lose their leaves (Janzen 1986a).

Soil classifications include entisols, inceptisols, mollisols, vertisols, and alfisols (Gerhardt 1994; Harris et al. 1971). Soils are developed from volcanic ignimbrites and consist of Non-Calcic brown soils (Alfisols; Harris et al. 1971) with medium to moderately light texture, that are well to excessively drained, and have low fertility (Vasquez Morera 1983). In early studies, the influence of soil conditions on the direction of succession was stressed (Whittaker 1953). More recently, permanent deflection of succession by soil disturbance is seldom suggested (Harcombe 1980). Harcombe (1977) suggested that the decrease of available soil nutrients due to disturbance does not strongly affect ecosystem recovery and that vegetation is independent of soil nutrients over a wide range (also Knight 1975). Denslow (1980a) pointed out that species with non-random distributions, such as those in a tropical dry forest (Hubbell 1979), often show no association with variation in soil conditions. Gerhardt (1994) provides a detailed comparison of soils between pasture and intact forest.

Since the late 1500's most of the upper plateau has been deforested for agriculture and pastures. The last time forests were selectively logged (e.g. *Swietenia macrophylla*) or cleared for pastures was in the 1940's (Janzen 1986b). Cattle were finally removed in 1978 and an active fire-control program was initiated in 1984. The disturbance history of the park has resulted in a mosaic of various stages of regeneration. Local authorities believe that the park's original forest consisted of mostly semi-evergreen trees (Janzen 1986a, b).

Cattle grazing and dry season grass fires within the park may have inhibited regeneration in the past and reduced the viable seed pool in the soil (Skoglund 1992). Removal of stress factors, such as fire and grazing, initiates regeneration of tropical forests (Lugo 1988). However, Janzen (1988a) suggested that grazing might have helped succession since it reduced sapling competition with the introduced jaragua grass (*Hyparrhenia rufa*) and reduced the amount of fuel for fires. Almost all fires in tropical

dry forest (and tropics in general) are anthropogenic (Budowski 1966; Vogl 1977; Janzen 1988a; Murphy and Lugo 1986a) and therefore are not a part of the natural disturbance regime. Janzen (1986a,b) suggested that in normal years in Santa Rosa, fire does not penetrate forests where regeneration has produced an overstory canopy, and only burns grasses, dead wood, and forest litter (also pers. obs.).

Data Collection

In January of 1996 I chose 13 patches of forest as study sites from aerial photographs and subsequent ground truthing in Santa Rosa National Park, Costa Rica. Most patches were homogenous in age (D.H. Janzen pers. comm.) with the exception of *Cuatro Esquinas* that contained a small ravine of older forest (Table 2-1). Although patch areas varied (mean = 35ha, range 22-56ha, Table 2-1, Fig. 2-1), all patches were connected with other forest and were close to mature forests for seed sources. Furthermore, the areas of patches were not correlated with forest age ($r = 0.385$, $p = 0.24$).

When studying stages of succession simultaneously one has to assume that all sites were originally similar, and the same succession processes proceeded at similar rates for all sites. The greatest distance between two sites was about 8 km (minimum 600m). The rate of succession to a mature successional stage is positively related to availability of propagules from old-growth forests (Rico-Gray 1991; Rico-Gray & Garcia-Franco 1992; Purata 1986), abundance of existing vegetation, and the type and intensity of disturbance (Janzen 1986a, Gerhardt & Hytteborn 1992; Purata 1986). Janzen (1986a) suggests that regeneration in Santa Rosa is rapid due to the proximity of the regenerating areas to forest fragments.

The topography of the upper plateau of Santa Rosa is undulating; all sites appear to have similar representation of aspects and slopes. Ages were known for sites that were abandoned within the past 40 years, and estimated for older sites by talking to local people, park botanists, and park historians. I could not calculate forest ages from annual growth rings since most species of tropical trees do not form these rings (Lieberman and Lieberman 1985). Two relatively intact forests were chosen as representatives of climax forest. I assigned their ages based on average turnover rates for other Central American

tropical forests (118 ±27 years in La Selva, Hartshorn 1978; 114-159 years on Barro Colorado Island, Brokaw 1982; and 137 years on Barro Colorado Island, Lang and Knight 1983). Because one of the sites had 6 large trees removed within the last century it was assigned a slightly younger age (110 years) than the other (130 years).

A 600m transect was surveyed within each of the 13 sites along a random compass bearing (Fig 2-1) with the restriction that the transect must remain within the forest patch. The same transects were used to study the influence of forest regeneration on primate densities (*Chapter 3*). All stems within 10m of either side of the transect and ≥ 5cm diameter at breast height (dbh) had their dbh measured, height estimated, and were identified to species. To aid in follow-up studies, Global locations (points) were recorded at 50m intervals with Trimble GeoExplorer hand-held GPS units. At least 180 positions were recorded for each point and averaged to give an accuracy of ± 2m for each point. It became apparent from the two dimensional GPS positions that most transects were not exactly 600m long ($\bar{\chi}$ = 558m, SE = 7). A total of 14.5 ha of forest was sampled. About 60 species of plants could be identified in the field; vouchers were collected from trees that were unknown and later identified by park botanists. Nomenclature used in this manuscript is from Janzen and Liesner (1980).

Data Analysis

Species Composition

Basal area (BA) was calculated for each tree from its dbh ($BA = \pi(dbh/2)^2$). Basal area is more directly expressive of species importance than density (Whittaker 1965); therefore summed basal areas were used as response variables for each species in a detrended correspondence analysis (DCA; CANOCO program, Ter Braak 1987). The DCA was used to evaluate the similarity in species composition between study sites. Correspondence analysis is similar to principal components analysis (PCA) except that correspondence analysis assumes bell-shaped, unimodal species response curves to environmental gradients rather than linear responses (Ter Braak 1995). Detrending is

used to make sure the second environmental axis extracted from the species data is not superficially correlated with the first axis (Ter Braak 1995).

To simplify the large data set (113 species), I only used species in the DCA that were non-vines (110 spp.), found in more than one site (85 spp.; Webb et al. 1967, 1970), were canopy or subcanopy species (73 spp.), and constituted more than 0.3% of the overall density (47 spp.; Knight 1975) or more than 0.5% of the summed basal area/ha (6 spp.). These constraints reduced the data set to 53 species. I used tree size cut-offs (non-understory and BA) because Webb et al. (1967) found that large tree species alone can explain almost all of the variation in all species. The response variable (summed basal area/ha) was log transformed to place less emphasis on sites where a particular species had high abundance. Four environmental variables were included in the DCA for each site: age (years since abandonment), mean dbh, canopy height (mean tree height), basal area/ha (BA), and density (stems/ha of all species). Within the DCA calculation, the four variables were correlated with site scores after the ordination (indirect methods). I was more interested in examining the associations of species with environmental variables than on using environmental variables to control for species variance (direct methods, e.g. DCCA).

Species were classified (Appendix 1) according to leafing (deciduous vs. evergreen), fruit dispersal (animal vs. wind), and leaf type (compound vs. simple), using information in Frankie et al. (1974), Croat (1978), Janzen and Liesner (1980), Opler et al. (1980a), Gentry (1982), Janzen 1983, and Janzen and Waterman (1984). 'Evergreen' species were those which maintained leaves for *ca.* 11.5 months/year (Janzen and Waterman 1984). Only canopy species (see *Structure*) were used when analyzing leaf and dispersal characteristics because wind dispersal is rarely found in smaller trees (Opler et al. 1975, Howe and Smallwood 1982) and leaf retention of smaller trees often depends on the amount of shade received from the canopy (Givnish 1978).

Several response variables were used in regressions against the estimated ages of the sites. Response variables included species richness (number of species) and diversity (Shannon-Wiener index, Krebs 1989), the proportion of canopy trees with simple vs. compound leaves, the proportion of canopy trees that are evergreen vs. deciduous, and the

proportion of canopy trees with wind vs. animal dispersed fruits. Unidentified species were included in species richness and diversity calculations but not in variables requiring knowledge of species characteristics; such as the percentage of trees with evergreen leaves.

Structure

Although strata are hard to distinguish in tropical dry forest (Frankie et al. 1974), it became apparent that forest structure could not be analyzed with all species pooled together. Species were classified (Appendix 1) as understory (<8m tall), subcanopy (8-20m), and canopy trees (≥21m) according to their maximum height (modified from Swaine and Whitmore 1988) and descriptions in the literature (Croat 1978; Janzen and Liesner 1980; Opler et al. 1980a; Janzen and Waterman 1984).

Several response variables were regressed against forest age including: mean dbh, canopy height (mean height of adult (≥10cm dbh, Herwitz 1981; Fleming and Williams 1990; Sabogal 1992) canopy trees), density (stems/ha of all trees), and basal area/ha of canopy trees.

Regression analysis assumes that the independent variable is known without error (Zar 1984) which was not true for forest age estimates. However, this rule is often impossible to adhere to and regression statistics are known to be robust to violations of this assumption (Zar 1984). Furthermore, forest ages were assigned prior to any data collection to avoid observer bias. Within the next year, species-specific growth curves will be available for most of the common tree species (B. Enquist pers. comm.) and I will then be able to assign more precise age estimates for each forest patch.

Types of regression models (e.g. linear or polynomial vs. growth) were chosen by examining residuals and selecting models with an even distribution of residuals above and below the fitted line (Zar 1984). Higher order polynomial equations were compared statistically to lower order polynomials and linear regressions to make sure they explained significantly more variation (Zar 1984: 365); in all cases the presented model explained significantly more variation ($p < 0.0255$) than the next lower order model. I could not find a statistical test to compare explained variation between linear or polynomial models and

growth models; therefore residuals were examined visually and coefficients of determination (R^2) were compared to select the most suitable and explanatory model.

RESULTS

A total of 13,653 stems greater than or equal to 5cm dbh were measured consisting of 113 known species (28-65 species per site), 96 genera, and 47 families. The 47 unknown species were found at a rate that ranged from 1 to 8 unknown species per site. Unknown species within each site were confirmed to be separate species; however, many of the 47 species may be duplicates between sites.

Species Composition

Axis 1 (A1) of the DCA explains a clear regeneration sequence in species composition (42.8%, Eigenvalue = 0.344), while A2 explained very little variation (3.9%, Eigenvalue = 0.128)(Fig. 2-2). Environmental variables explained most of the variation in A1 (species-environment correlation coefficient = 0.926); however, forest age was the only single environmental variable that explained significant variation in A1 (t = 3.38, 7 df, p = 0.011; Fig. 2-2).

A1 species scores were sorted resulting in a list of plant species ranked according to their location on the regeneration gradient (Table 2-2). Ordination analysis assumes Gaussian bell-shaped curves for each species along the gradient with widths of 4 standard deviations; therefore, sites have completely different species composition and species do not co-occur if their scores differ by 4 (Ter Braak 1995). Nonetheless, species scores are the average location of the species on the regeneration gradient and can indicate trends even with short gradient lengths.

The rate of change in species composition decreases with regeneration as seen in the regression of forest age against A1 site scores (growth model, Fig. 2-3). The large changes in A1 for forest ages less than 30-40 years suggests that species shifts occur at a higher rate before 30-40 years of age than after.

Species richness peaked early in regeneration and then leveled off (cubic polynomial model, Fig. 2-4). Species diversity leveled off after 40 years of regeneration (growth model, Fig. 2-4). By arbitrarily dividing the species into early (A1<2), mid- (2-3), and

mature successional species (>3) I examined the extent to which each group contributed to the high species richness after 40-70 years of regeneration. Species richness of early successional species decreased with time (quadratic polynomial model, Fig. 2-5), that of mid-successional species peaked in forests 50-90 years old and then declined (quadratic polynomial model , Fig. 2-5), and that of mature forest species increased linearly through time (Fig. 2-5). On Figure 2-5, the intersection of the regressions from the early and mature successional species, along with the peak in mid-successional species, suggests that a mixture of the three groups is the reason for high species richness in forests 50-70 years old.

The proportion of canopy trees that had simple evergreen leaves increased with the age of the forest (R^2 = 0.865, p = 3.98 x 10^{-6}; Fig. 2-6). However, there was no trend through succession for the proportion of trees with compound evergreen leaves (*Andira inermis* and *Hymenaea courbaril*, p = 0.366; Fig. 2-6). The proportion of canopy trees that had simple (R^2 = 0.252, p = 0.080) or compound (R^2 = 0.469, p = 0.010) deciduous leaves decreased with the age of the forest (Fig. 2-7). The proportion of canopy trees with wind-dispersed diaspores decreased with the age of the forest (R^2 = 0.350, p = 0.033; Fig. 2-8) while the proportion with animal-dispersed diaspores increased (R^2 = 0.340, p = 0.037; Fig. 2-9).

Structure

All 13 sites had negative exponential distributions of dbh (Fig. 2-10). Regressions of mean tree height, mean dbh, and basal area leveled off (growth model) after 40-60 years of regeneration (Fig. 2-11 - 2-13). Density of trees was highest in forests 20-40 years old (Fig. 2-14).

DISCUSSION

Species Composition

The regression of Axis 1 against estimated forest age indicates that the rate of change in species composition decreases as the forest matures (see also Shugart and Hett 1973; Purata 1986) thus approaching a stable species composition (Whittaker 1953; Odum

1969). The rate of change in species composition would be much slower in the older sites if age estimates for the three older sites are underestimates, i.e. very small differences in species composition relative to large differences in age.

Species diversity increased in the first 40 years and then leveled off. This trend appears common in tropical forests (Knight 1975; Purata 1986; Brown and Lugo 1990; Rico-Gray and Garcia-Franco 1992). Species richness peaked in forests 50-70 years old resulting from a combination of early, mid, and late successional species; this supports the intermediate disturbance theories of Connell (1978).

Denslow (1980a, b) suggested that the majority of species in a community will be adapted to grow and establish in the most common forest types, and species diversity will be highest at forest ages produced by the historic frequency of disturbance. The current study provides contradictory evidence using these two criteria. The majority of the tree species exhibited high association with the oldest forest (Table 2-2) suggesting that old mature forest was the most common forest type in the past. However, the high species richness in 50-70-year-old forests agrees with the fact that Santa Rosa has frequently been disturbed in the past (see Rico-Gray and Garcia-Franco 1992) and now contains a high proportion of pioneer species. Among these pioneers, many are exotic species from human disturbance (Denslow 1980b; Skoglund 1992) which may alter the natural course of succession and the resulting forest structure (Janzen 1986b). In areas where large-scale *natural* disturbances are rare, such as tropical dry forest (Hubbell 1979), the proportion of species that could colonize an abandoned pasture should be limited to a few gap-specialized species (Denslow 1980a, b).

Species richness is higher in intermediate stages of succession when both early and late successional species are present (Fig. 2-4 - 2-5; Horn 1974). The peak in species richness is probably due to the successful establishment of shade-requiring species under the quickly developed canopy of pioneer species (Uhl 1987; Gerhardt 1994; Lieberman and Mingguang 1992).

The DCA was very useful at describing each species' association with regeneration. *Enterolobium cyclocarpum* had the highest association with the most recently abandoned pastures. This no doubt results from the seeds being cattle/horse dispersed; there is almost

no current reproduction from seed in the park (Janzen 1983). *Cordia alliodora*, a pioneer tree that reaches mature size in 15 years of growth (Opler et al. 1975; Budowski 1993), had highest association with sites 14-25 years old. *Byrsonima crassifolia* (Janzen 1983), *Guazuma ulmifolia* (Janzen 1983; Fleming and Williams 1990), *Acrominae vinifera* (Janzen 1983), *Spondias mombin* and *S. purpurea* (Janzen 1985; Herwitz 1981), and *Cochlospermum vitifolium* (Frankie et al. 1974; Janzen 1983) have all been described as associated with early successional forests and were ranked low on A1. *Sapranthus palanga* mature in 75-100-year-old secondary successional forest (Janzen 1983). *Hymenea courbaril* (Bazzaz 1991), *Brosimum alicastrum* (Peters 1991), *Slonea terniflora*, *Manilkara chicle*, *Mastichodendron capiri* (Janzen 1986a) have all been classified as mature forest canopy species. Likewise, gap species such as *Cercropia peltata* (Fleming and Williams 1990) and possibly also *Zuelania guidonia*, *Apeiba tibourbau* (Herwitz 1981), and *Annona purpurea*, were most associated with late successional sites. The lack of similarity in species composition between early successional and mature forest is probably due to the reduction of the soil seed bank by intense and long term pasture use of the area, and differences in the optimal gap size for establishment and regeneration (Denslow 1980a, b; Pickett 1983; Fleming and Williams 1990).

Species Characteristics and Regeneration

Opler (1978) pointed out two strategies of trees in succession: 1) trees with compound, deciduous leaves and wind dispersed diaspores; and 2) trees with simple, evergreen leaves and fleshy, animal dispersed fruit. A large proportion of canopy trees on my study sites (41% of the trees, 51% of the species) fall into one of these two strategies. Many researchers (e.g. Odum 1969, Opler et al. 1977; Opler 1978) have classified species along a successional gradient as r- or K-selected following the theory proposed by MacArthur and Wilson (1967). Species found most often in early successional forest in Santa Rosa appear r-selected: high reproductive rate (occur at high density), long-distance dispersal (wind-dispersed seeds), high quantity dispersal (dehisced seeds), high growth rate (leveling off of dbh and canopy height within 40 years), and opportunistic

(deciduous). The oldest communities in Santa Rosa are dominated by species with moderate density, with high 'quality' dispersal (fleshy/animal dispersed, Opler et al. 1980b), and constant maximizers of resources (evergreen).

Wind dispersal allows pioneer species to colonize large gaps in the forest such as abandoned pastures (Opler et al. 1980b; Janzen 1988a). Ground fires and long term use of the area as pastures probably significantly reduced the viable seeds of mature forest species in the soil and now abandoned pastures must be recolonized by wind dispersed species (Gomez-Pompa et al. 1972; Uhl 1987; Sabogal 1992). An exception is when shade trees are left for cattle, as is the case of my study site 'Park Boundary Road' (Fig 2-10). These residual trees are very common in Guanacaste and give perching sites for birds and shade for terrestrial animals, thereby speeding succession toward a more animal-dispersed species composition (Fig. 2-9; Janzen 1988a; Guevara et al. 1986).

In the past, researchers have accounted for the dominance of evergreen species by soil moisture, aspect, and topography (Janzen and Waterman 1984; Murphy and Lugo 1986a; Sobrado 1991; Borchert 1994); however, these factors are rarely quantified and these studies often ignore successional differences between study sites (Borchert 1994; but see Gerhardt 1994). Furthermore, soil characteristics such as carbon, nitrogen, depth, and moisture, develop rapidly in response to the vegetation and therefore change through succession (Drury and Nisbet 1973; Harcombe 1980). There is little doubt that soil moisture influences leaf drop within species (Bullock and Solis-Magallanes 1990, Olivares and Medina 1992, Borchert 1994) but I have not found a study suggesting that soil moisture influenced the relative dominance of evergreen and deciduous species.

Several studies have suggested that evergreen species have higher ability to tolerate water stress than deciduous species (Sobrado 1986; Fanjul and Barradas 1987). Sobrado (1986) attributes the dominance of evergreens to their deep root systems and utilization of subsoil water compared to the shallow root system of deciduous trees. It is probably the slow consistent growth, constant photosynthesis, and long life (Opler 1978) that allows evergreens to competitively exclude or outlast deciduous species after several decades. My study suggests that evergreen trees will eventually dominate the upper

plateau of Santa Rosa in the absence of major disturbance (Figs. 2-6 and 2-7, and see Budowski 1970; Janzen 1986a).

In Santa Rosa National Park, the proportion of trees with compound leaves decreased with regeneration of the forest. Givnish (1978) suggests that compound deciduous leaves are adaptations for desiccation avoidance and rapid growth. By regularly shedding the smallest twigs (rachis of the compound leaf) the tree reduces its surface area/volume ratio (desiccation avoidance) and promotes vertical growth instead of horizontal branching. This study supports the hypothesis that compound leaves are adaptive to early succession so long as the tree is deciduous, and that the reduction of surface area during the dry season is adaptive to early succession. These are probably adaptations to high evaporation in abandoned pastures and rapid vertical growth of shade-intolerant species (Givnish 1978).

Forest Structure

It is evident from the structural variables (mean dbh, canopy height, density) that the age of older forests cannot be predicted from their structure due to the leveling off of many variables. Basal area increases with succession but is highly variable between sites (Fig. 2-13). It appears that most structural changes in tropical dry forest occur within the first 40 years, similar to biomass changes (Brown 1980). Sixty-year-old tropical dry forest has higher aboveground biomass than mature forest (Brown 1980; Brown and Lugo 1980, 1982).

In the past, trees in middle to late successional forests were thought to have very low mortality and regeneration until senescence of the oldest trees in the climax forest (Hartshorn 1978). Knight (1975; also Whittaker 1953) suggests that negative exponential distributions of size classes will be evident in very young and mature forests, but not in mid-successional forests. However, later studies found that mortality of trees >10cm dbh in mature forest is independent of the age (dbh class) of the tree (Swaine et al. 1987; Leigh and Smythe 1978; Lieberman et al. 1985; Lieberman and Lieberman 1987). If one assumes that when a tree dies it is replaced by juveniles, age independent mortality would result in negative exponential size class distribution in all stages of succession, such as in

the current study (see also Chapman and Chapman 1990; Rico-Gray and Garcia-Franco 1992; Larose 1996).

One problem with studying patches of forest in Central America is that most sites have been selectively logged (high-graded). Hartshorn (1978) suggests that high-graded forests will have fewer gaps and therefore fewer juvenile trees than intact climax forest. This study shows little difference in size class distributions between heavily high-graded and intact mature forest (Fig. 2-10; Table 2-1); therefore high-grading has had little effect on forest structure. Johns (1985) also found no change in the size distribution or species composition following high grading. High-grading caused a change in the basal areas and spatial distributions of trees, but random destruction of all sizes and species of trees during the removal of harvested trees returned the forest to original species composition and size distribution (Johns 1985).

Management Implications

This study suggests that tropical dry forest in Pacific Central America can regain its structure and species diversity within a century through natural regeneration, at least in areas where enough of the original forest remains to provide seed sources. Human intervention is probably needed in areas of large-scale disturbance where natural dispersal of propagules is insufficient (Lugo 1995).

The negative exponential size class distribution of tropical dry forest indicates good conditions for sustained production and human utilization (Sabogal 1992). Sabogal (1992) lists many of the species of trees in Santa Rosa as used by humans for timber, firewood, fruits, and medicines. Opler and Janzen (1983) suggest *Cordia alliodora* as a quick growing early successional tree with fine wood for furniture and lumber. *Gliricidia sepium* has extremely hard wood and is well suited for fence posts and house supports (Janzen 1983; Budowski 1993). The heartwood of *Pithecellobium saman* is sought for furniture and wood paneling (Janzen 1983). Sustainable use of secondary forests will help to avoid deforestation of primary forests (Brown and Lugo 1990); however, much more research is needed to develop sustainable management plans for tropical dry forest.

Lately there is a trend to de-emphasize the importance of species composition and manage forests for structure and biodiversity (Frumhoff 1995, Lugo 1995). If this is the desired option, tropical dry forest can regenerate their structure and diversity within 40-50 years. Brown and Lugo (1990) suggest that after 50-80 years the system has reached a steady state where several turnovers of organic matter has occurred and the net ecosystem productivity rapidly approaches zero. On the other hand, species composition is just as important, if not more important, to conserve as species diversity or forest structure. This study suggests that a large proportion of the dominant tree species are associated with undisturbed forests; therefore management plans will need to incorporate long return intervals between forest disturbances to maintain areas with mature forest species composition.

Knowledge of species associations with different successional stages is key to developing management plans (Oldeman and Van Dijk 1991). While studies on individual species reveal much more detailed information, comparisons of different communities quickly expose the associations of a majority of tree species with succession. Only by understanding these associations can managers plan strategies and set management goals (Oldeman and Van Dijk 1991).

Early successional forests dominated by wind dispersed deciduous trees offer little food for frugivorous wildlife (Janzen 1988a). In the dry season, these deciduous trees will offer no leaves for folivores, and during the wet season few of these species have ripe fruit or seeds (Janzen 1988a). Furthermore, wind dispersed seeds are often toxic or escape predation by self-burial in the litter (Janzen 1988a). The influence of forest regeneration on wildlife population characteristics and sizes is the next step in tropical dry forest research.

Table 2-1. Location and disturbance histories of the 13 study sites. Ages (range in parenthesis) older than 40 yr are estimates from park historians, park botanists, and local people. Two sites were relatively intact and arbitrarily given ages based on published turnover rates of similar forests. Site numbers refer to locations on Figure 1-1.

#	Name	Age	Area (ha)	History
3	Park Boundary Road	10	26	Burned in 1986, rice field in early 1960's.
2	Camino Los Barrachos	14	31	Pasture before burn in 1982.
6	Quebrada Duende	20	29	Divided by old cart track to Liberia. Far east of the Casona. Grass fire in 1991.
5	Quebrada Guapote	25 (19-30)	44	Officially abandoned in 1977. Transect runs north from fire road parallel to Hacienda Rosa Maria.
7	Cerco de Piedra	40	22	Transect outside stone wall enclosure. Pasture prior to late 1950's.
4	Laguna Escondida	40	56	Abandoned pasture south of man-made laguna
8	Cuatro Esquinas	50 (40-70)	50	Heavily logged in 1940's. On border of park with Hacienda Rosa Maria. Transect crosses small ravine of older age (70-100).
9	Tocon	60 (40-70)	40	Heavily logged in 1940's for fence posts
11	Loma	70 (60-80)	31	Selectively logged in 1940's
10	Cuajiniquil	75 (60-90)	38	Selectively logged in 1940's for fence posts. Appears less disturbed than Loma.
12	Mirador de Naranjo	95 (80-100)	32	Lightly selectively logged in 1940's.
14	Bosque Humedo	Relatively intact (110)	27	Six trees were logged in the late 40's. Hilltops may have been damaged by wind.
13	Quebrada Puercos	Relatively intact (130)	28	Part of transect is in the former Finca Jenny

Table 2-2. Species scores from DCA ranking species in order of association with older sites.

Species Name	Family	Axis 1	
Ixora floribunda	Rubiaceae	5.08	
Quercus oleoides	Fagaceae	4.85	110 - 130
Sloanea terniflora	Elaeocarpaceae	4.45	year old
Coccoloba guanacastensis	Polygonaceae	4.17	sites
Cercropia peltata	Moraceae	4.15	
Swartzia cubensis	Caesalpinaceae	3.97	
Eugenia salamensis	Myrtaceae	3.90	
Brosimum alicastrum	Moraceae	3.90	
Apeiba tibourbau	Tiliaceae	3.69	
Zuelania guidonia	Flacourtiaceae	3.53	
Karwinskia calderoni	Rhamnaceae	3.51	
Annona purpurea	Annonaceae	3.29	
Ocotea veraguensis	Lauraceae	3.24	
Simarouba glauca	Simaroubaceae	3.23	
Guettarda macrosperma	Rubiaceae	3.17	
Hymenaea courbaril	Caesalpiniaceae	3.10	
Luehea candida	Tiliaceae	3.08	
Manilkara chicle	Sapotaceae	3.07	
Mastichodendron capiri	Sapotaceae	3.02	
Astronium graveolens	Anacardiaceae	3.02	
Bombacopsis quinatum	Bombacaceae	2.78	
Licania arborea	Chrysobalanaceae	2.77	
Exostema mexicana	Rubiaceae	2.76	
Sterculia apetala	Sterculiaceae	2.75	
Ficus spp.	Moraceae	2.61	
Sapranthus palanga	Annonaceae	2.60	70 - 90
Annona reticulata	Annonaceae	2.57	year old
Bursera simaruba	Burseraceae	2.45	sites
Lonchocarpus costaricensis	Fabaceae	2.42	
Rudera trinvervis	Verbenaceae	2.38	
Calycophyllum candidissimun	Rubiaceae	2.37	
Cordia panamensis	Boraginaceae	2.36	
Tabebuia ochraceae	Bignoniaceae	2.34	
Cedrela odorata	Meliaceae	2.19	
Cochlospermum vitifolium	Cochlospermaceae	2.13	40 - 60
Chumelia spinosa	Rubiaceae	2.12	year old
Luehea speciosa	Tiliaceae	2.07	sites
Genipa americana	Rubiaceae	2.03	
Bursera tomentosa	Burseraceae	1.83	
Hemiangium excelsium	Hippocrateaceae	1.72	
Spondias mombin	Anacardiaceae	1.58	20 - 25
Spondias purpurea	Anacardiaceae	1.57	year old
Lonchocarpus acuminatus	Fabaceae	1.49	sites
Diaspirous nicaraguensis	Ebenaceae	1.23	
Cordia alliodora	Boraginaceae	1.17	
Acrominae vinifera	Palmae	1.16	
Lonchocarpus minimiflorus	Fabaceae	1.06	
Pithecellobium saman	Mimosaceae	0.99	10 - 14
Stemmadenia obovata	Apocynaceae	0.62	year old
Guazuma ulmifolia	Sterculiaceae	0.42	sites
Gliricidia sepium	Fabaceae	-0.22	
Byrsonima crassifolia	Malpighiaceae	-0.34	
Enterolobium cyclocarpum	Mimosaceae	-0.54	

Figure 2-1. Location of sites and transects in Santa Rosa National Park. Pasture site is used in analyses in Chapter 2.

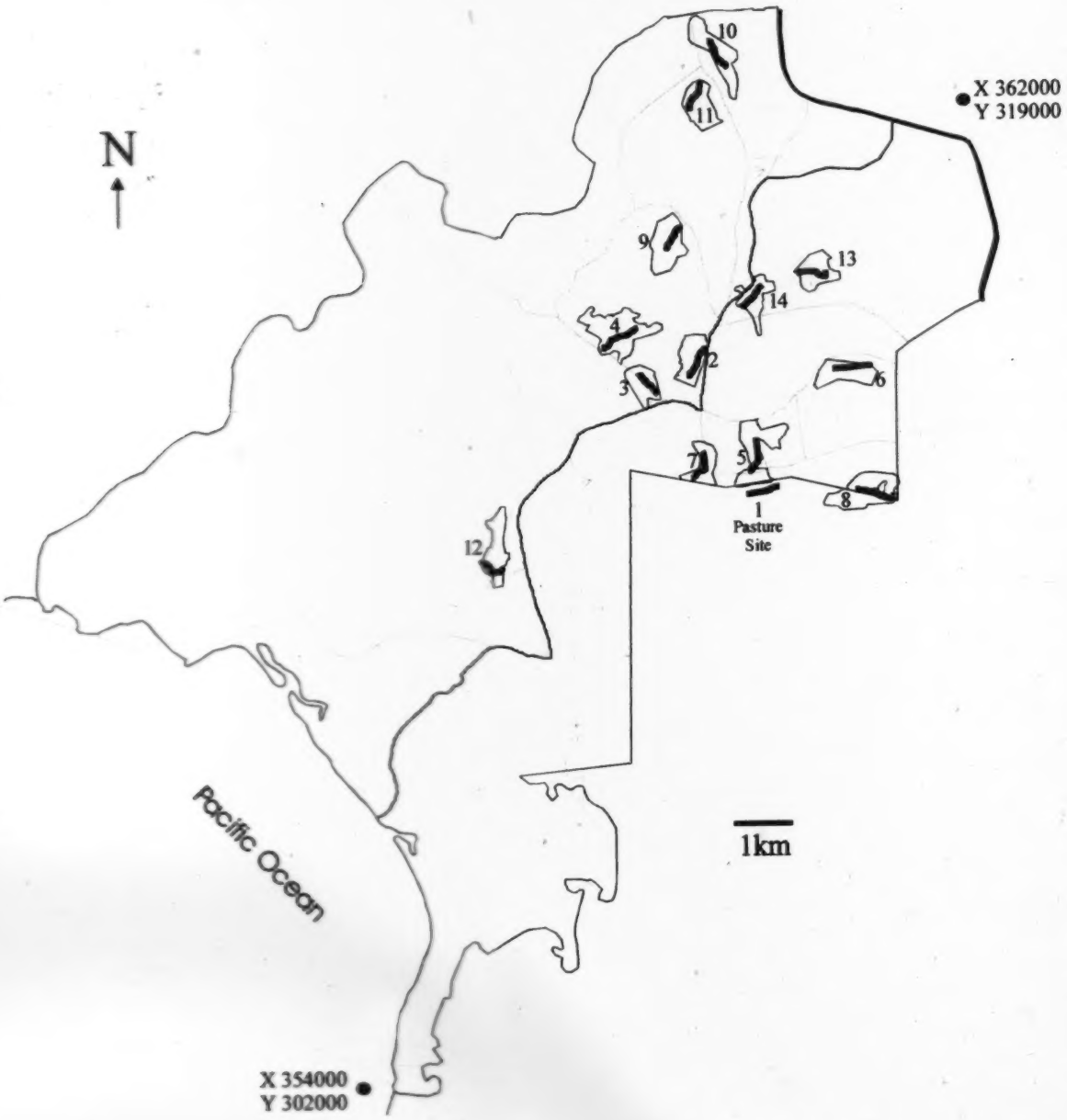


Figure 2-2. Plot of site scores from detrended correspondence analysis (DCA) based on species dominance (basal area / ha). Ages are beside each site (■). Length and direction of arrows represent the strength of the relationship between the environmental variables and the axes. Environmental variables were correlated with site scores after the ordination was calculated (indirect methods).

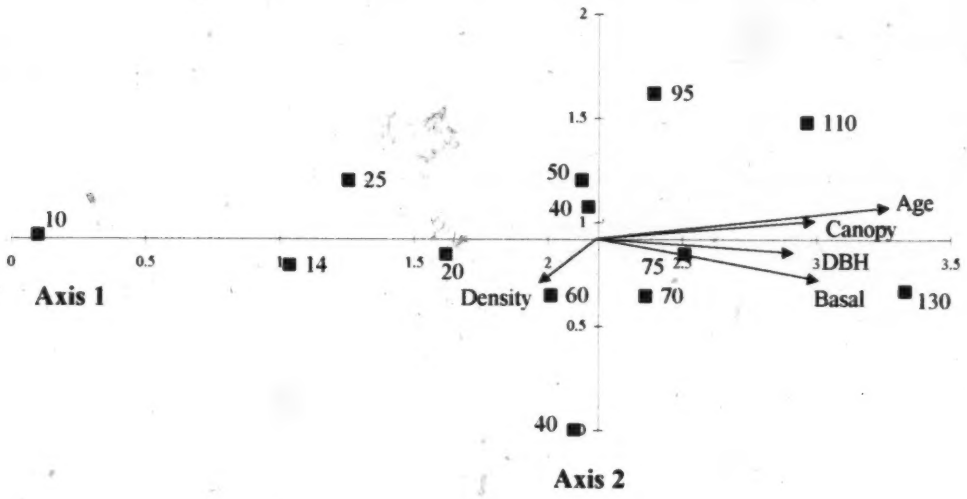


Figure 2-3. Species change along a regeneration gradient. Species change (succession) occurs rapidly within the first 40 years and then levels off. If ages for two oldest sites are underestimates, the plateau is more pronounced.

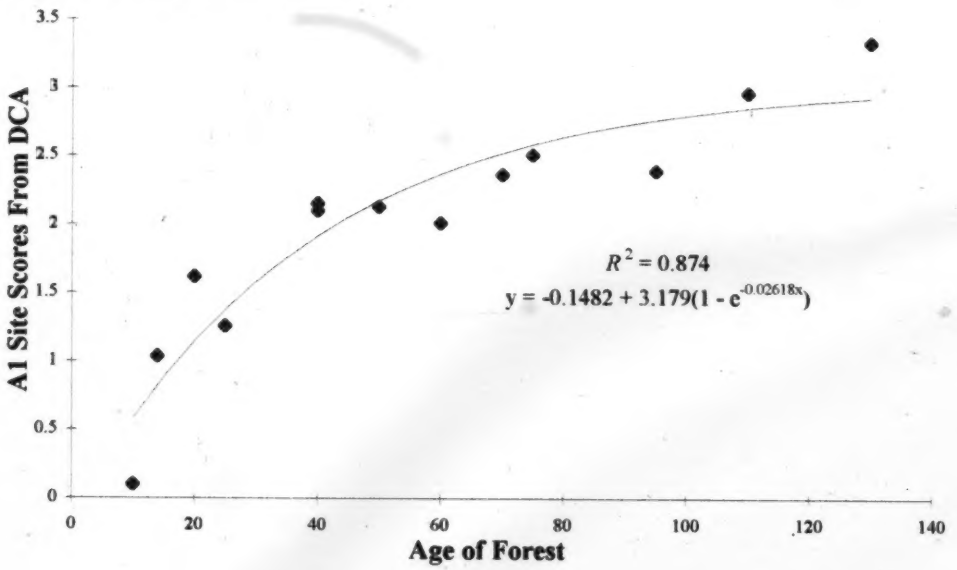


Figure 2-4. Species richness (◆) and Shannon-Wiener diversity (□) along a regeneration gradient. A cubic polynomial equation describes the peak in species richness at ages 40-80 years.

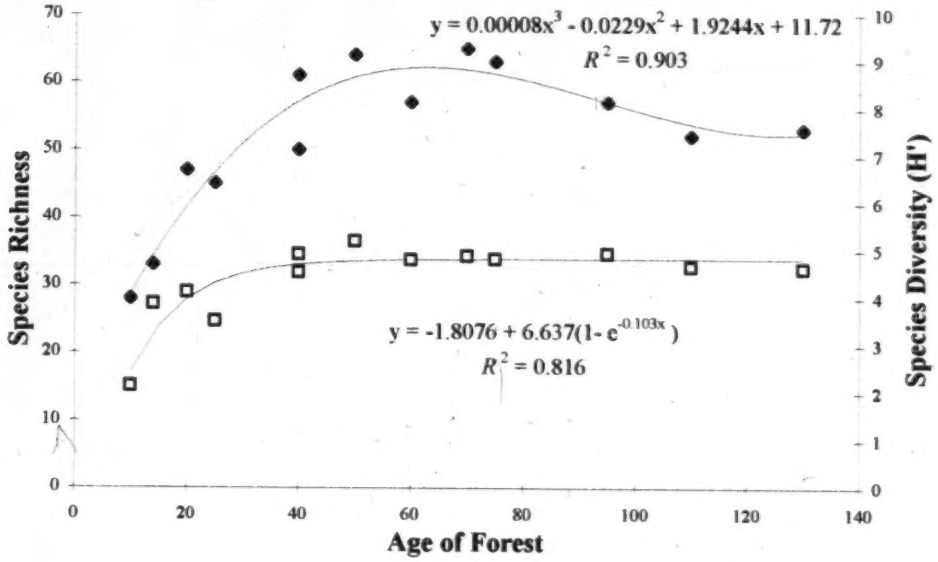


Figure 2-5. Species richness for early successional (▲), mid-successional (□), and mature forest species (n) along a regeneration gradient. Quadratic polynomial equations describe the early and mid-successional species, while mature forest species increase linearly with the age of the forest.

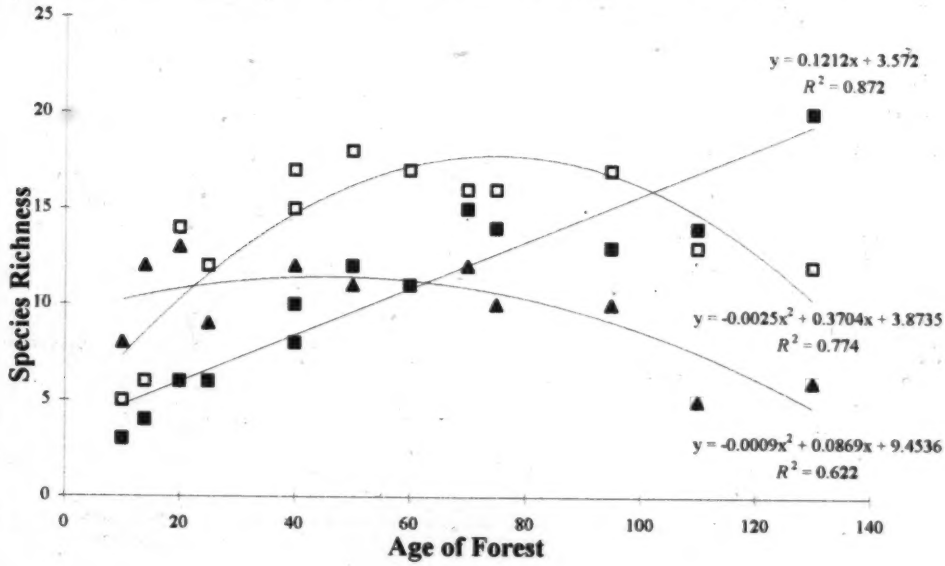


Figure 2-6. Proportion of canopy trees that are evergreen with simple (◆) and compound (□) leaves along a regeneration gradient.

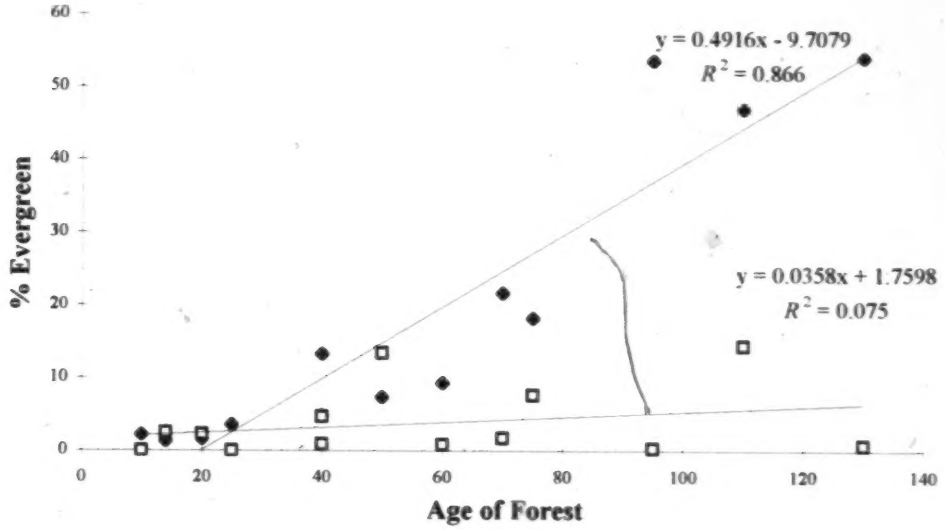


Figure 2-7. Proportion of canopy trees that are deciduous with simple (◆) and compound (□) leaves along a regeneration gradient.

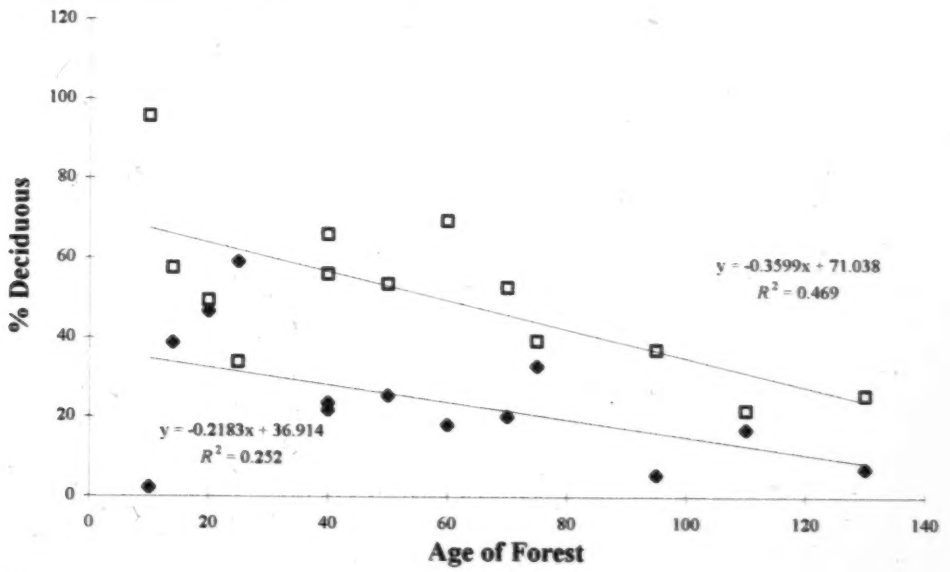


Figure 2-8. Proportion of wind-dispersed canopy trees along a regeneration gradient. Dominance of *Spondias mombin* and a few residual trees such as *Enterolobium cyclocarpum* influence the proportion of wind-dispersed trees in the youngest site.

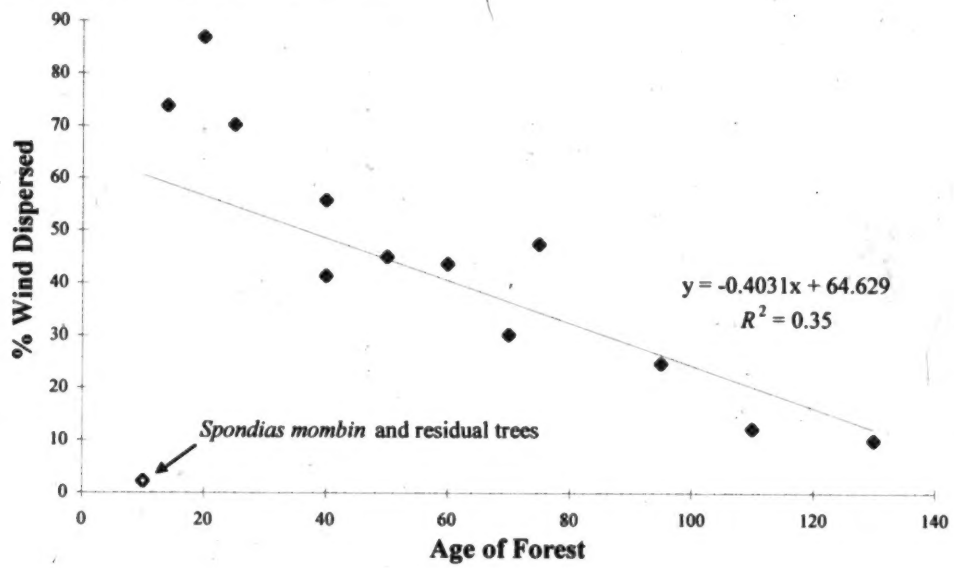


Figure 2-9. Proportion of animal-dispersed canopy trees along a regeneration gradient. Dominance of *Spondias mombin* and a few residual trees such as *Enterolobium cyclocarpum* influence the proportion of wind-dispersed trees in the youngest site.

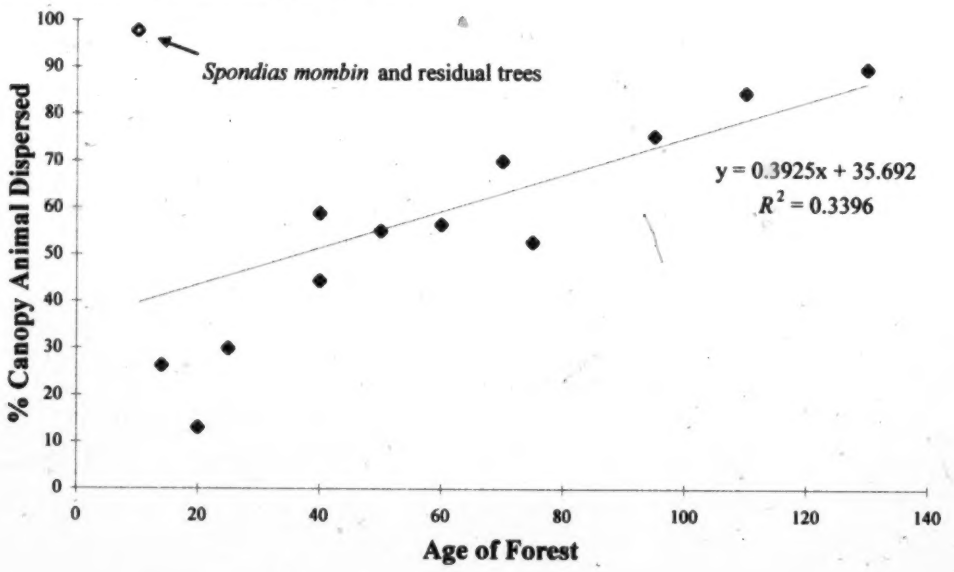


Figure 2-10. Size class distributions of canopy species in the 13 study sites ordered by age, top to bottom, as in Table 1-1.

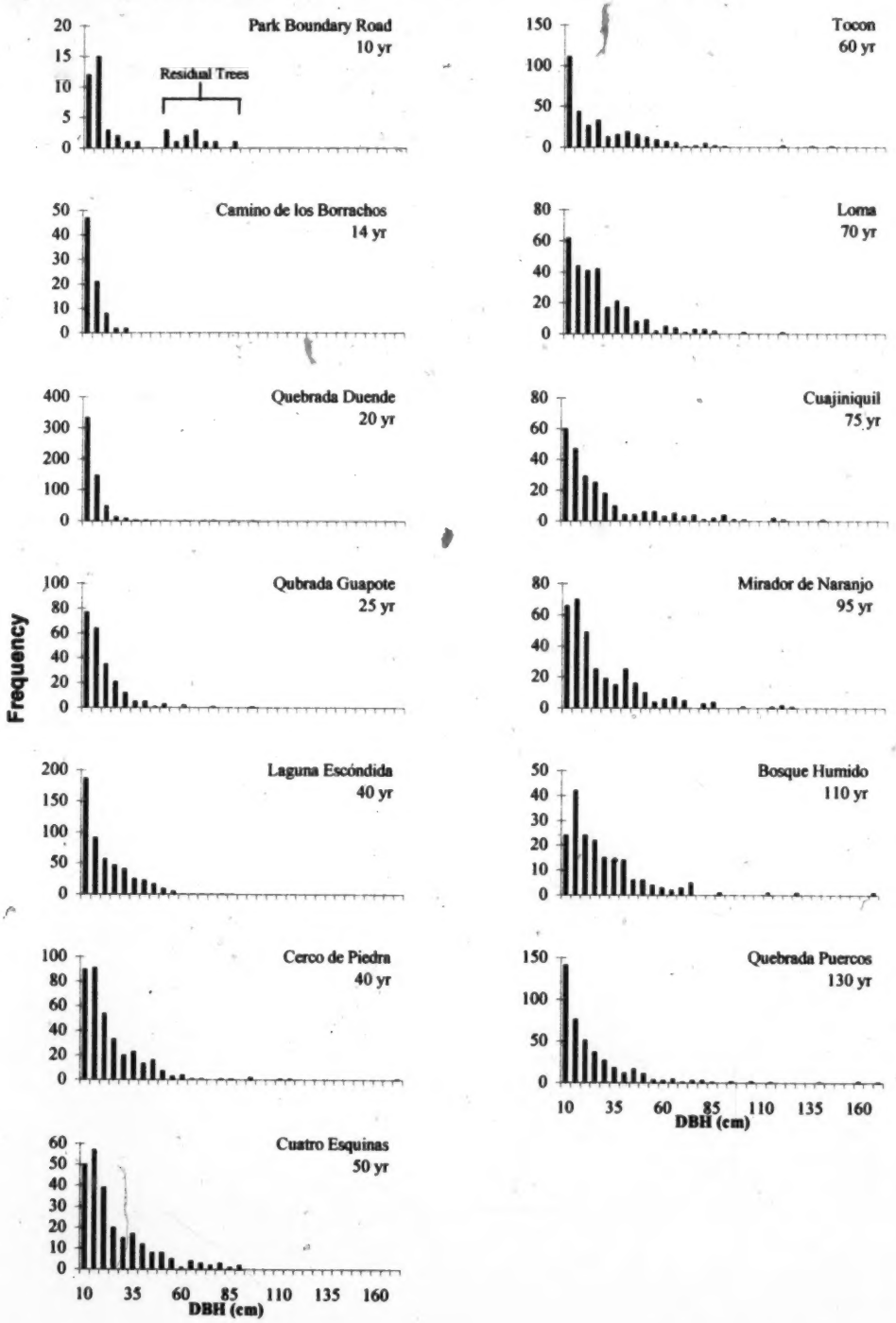


Figure 2-11. Canopy height (mean tree height of canopy trees >=10cm dbh) along a regeneration gradient.

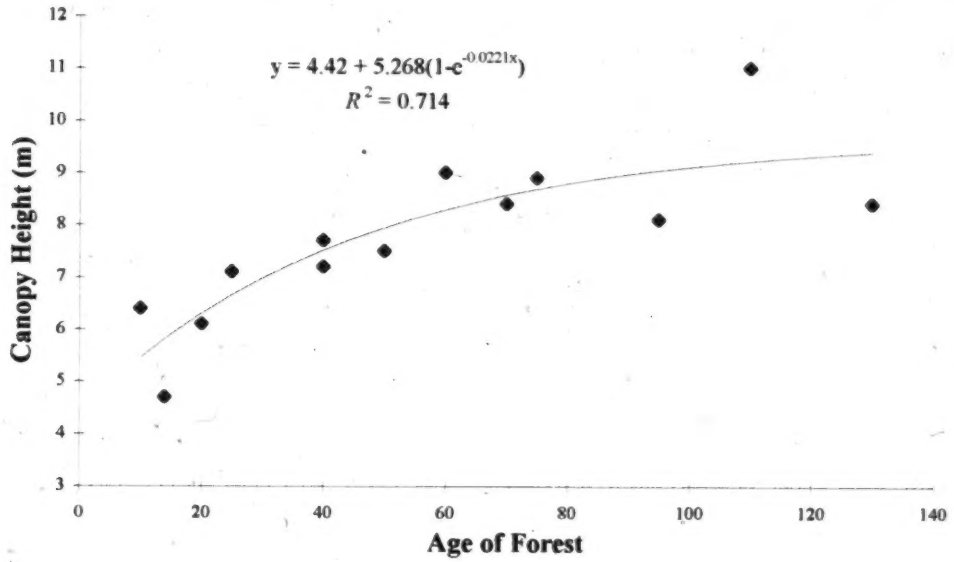


Figure 2-12. Mean dbh of adult (>=10cm dbh) canopy trees along a regeneration gradient. Residual trees left after pasture abandonment influenced the mean dbh in the youngest site (excluded from regression), and maybe also in one mid-aged site (Tocon).

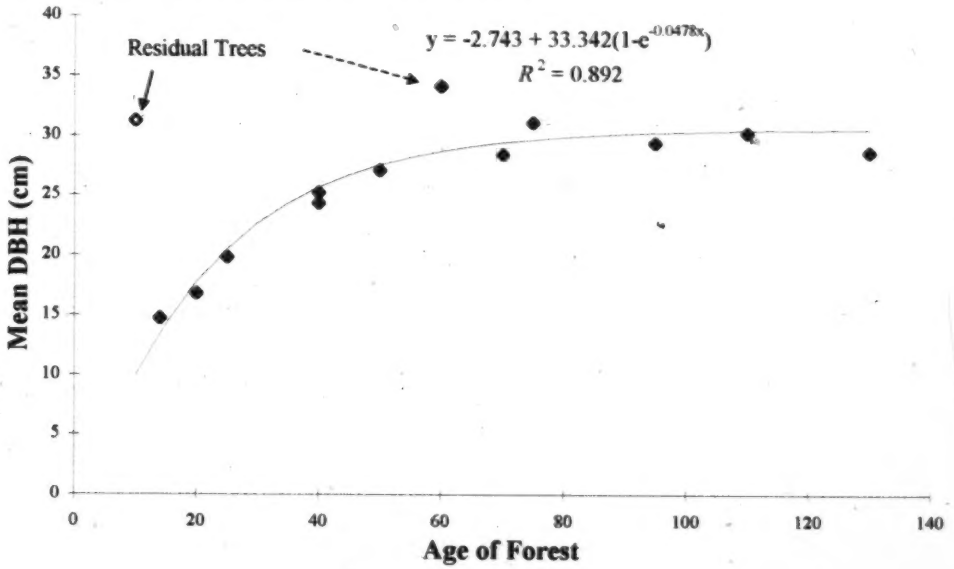


Figure 2-13. Basal area/ha of canopy tree species along a regeneration gradient.

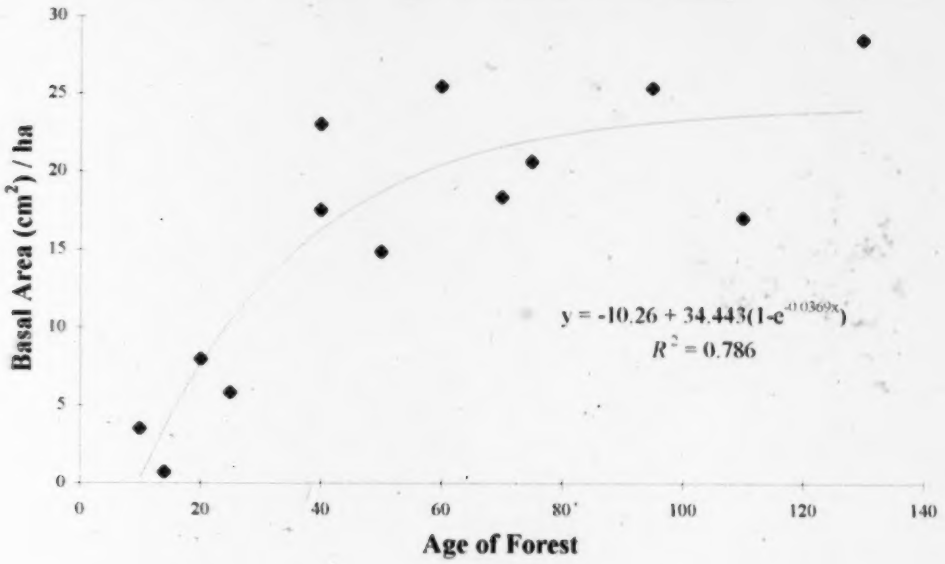
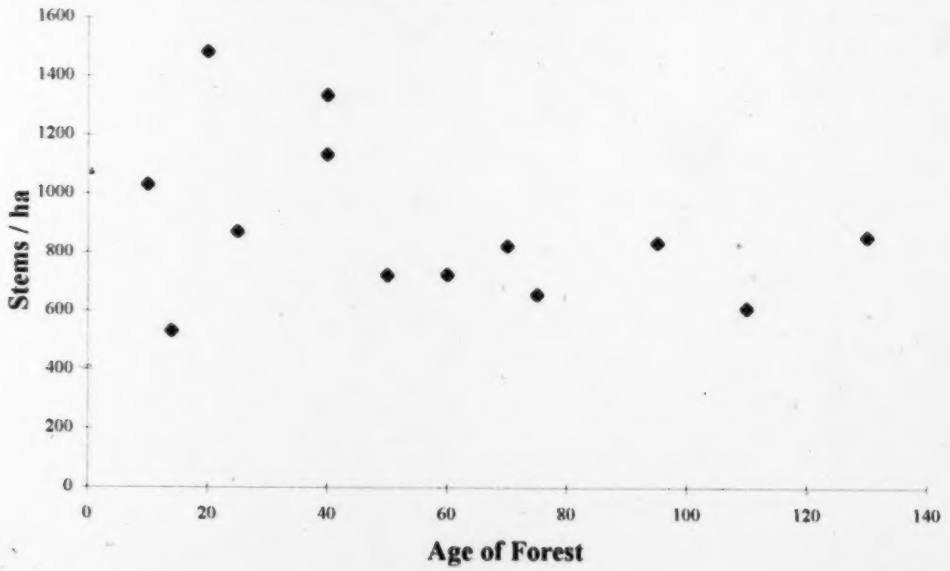


Figure 2-14. Density of trees (stems) along a regeneration gradient.



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III. Influence Of A Regeneration Gradient On Three Species Of Monkeys In Tropical Dry Forest

INTRODUCTION

Tropical dry forest once covered much of Central America but less than 2% of its original area is in an undisturbed state (Janzen 1986). Sustainable management plans for tropical dry forest is needed desperately to compensate for high deforestation rates and loss of wildlife habitat (Murphy and Lugo 1986; Frumhoff 1995). Unfortunately, land restoration and subsequent habitat regeneration is the only management option left for tropical dry forest. In chapter 2 I examined the changes in forest structure and species composition along a regeneration chronosequence of tropical dry forest. What remains to be answered is how this regeneration affects the wildlife within the forest, and whether regenerating forests provide adequate habitat to attract and sustain wildlife. Knowledge of densities of animals in various habitats is needed to construct effective conservation strategies (Eisenberg and Thorington 1973). Frumhoff (1995) stresses the importance of knowing the size and composition of viable wildlife populations and their ability to use disturbed forest as it regenerates. In this study I examine the influence of a regeneration gradient on the density and group composition of three species of monkeys, white-faced capuchins (*Cebus capucimus*), mantled howling monkeys (*Alouatta palliata*), and spider monkeys (*Ateles geoffroyi*), in Santa Rosa National Park, Costa Rica.

Forest age and stage of regeneration is rarely used to explain differences in densities, demography, or behavior of non-human primates (but see Fedigan et al. 1996, in press; Fimbel 1994; and Olupot et al. 1994). Recent long-term studies have demonstrated that over a large spatial scale, the number of capuchins and howlers are increasing in Santa Rosa as the park regenerates from abandoned pastures (Fedigan et al. 1996; Fedigan et al. in press). It is unlikely, however, that monkey densities are changing uniformly on a smaller spatial scale within the park. Heltne and Thorington (1976) refer to such differences as meso- and micro-distribution scales. Undisturbed forest patches probably

have very little year to year change in monkey densities; whereas rapidly regenerating forests probably have higher rates of change. Fedigan et al. (1996) found that the size of capuchin groups in evergreen [older] forest grew more slowly than groups in deciduous [younger] forest. Conservationists and managers need to know the stage of regeneration when primates return to a disturbed forest from local refugia, when changes in densities are occurring most rapidly, and when the population has returned to a pre-disturbance state. Without this information it is very difficult to estimate or predict available habitat and monkey population size. The current study examines monkey densities along a chronosequence of forest ages, and on a small scale to estimate the time required for monkey populations to recover from habitat disturbance.

The three species of monkeys in the park make possible comparisons of the influence of forest regeneration on different diets and group compositions. Many studies suggest that body size, proportion of fruit and flowers in diet, dietary specialization, and home range size are negatively related to the ability of a species to survive in disturbed forests (Freese 1976; Freese et al. 1982; Johns 1985a, 1992; Skorupa 1986; Johns and Skorupa 1987; Bearder 1991). Similarly, insectivorous species may benefit from high insect biomass in secondary forests (Freese 1976; Lovejoy et al. 1986; Schwarzkopf and Rylands 1989). Based on these generalizations the order of species returning to a regenerating forest following disturbance should be capuchins, howlers, and spider monkeys respectively.

Both sustainable densities and viable group compositions must be the objective for management and conservation. There are many situations in which dense populations can occur with unnatural population composition; therefore estimates of age and sex structure as well as density are needed to assess population status and plan effective conservation strategies (Heltne andThorington 1976; Cant 1978). Age ratios are often used as indicators of a population's viability (Olupot et al. 1994) and several studies have shown differences between habitats (Butynski 1990) or as a result of population disturbance (Heltne et al. 1976), or habitat disturbance (Johns 1992). Similarly, sex ratios (Chapman et al. 1989a,b, 1990a) and group sizes may differ between habitats (Chapman and Balcomb in press). A few studies suggest that group size and the ratios of immatures to adults increase with

regeneration of habitat (Olupot et al. 1994; Fedigan et al. 1996, in press). Heltne et al. (1976) suggested that low group size, low male:female sex ratios, and low immature:adult female age ratios are all indicative of a recently stressed population. In this study I examine the changes in group age/sex structure and group size of each monkey species along a gradient of regeneration.

Although the time required for wildlife to recover from a disturbance is the primary question to be answered, managers are also interested in understanding what factors attract the primates and improve the quality of the habitat. Frugivorous and folivorous wildlife may be sensitive to changes in the proportion of trees with evergreen leaves and animal-dispersed fruits (*Chapter 2*). Food abundance is often assumed to influence primate density and group composition; however, attempts to correlate primate and food abundances have had mixed results (correlated, Skorupa 1986; no association, Coelho et al. 1976). Skorupa (1986) found that the abundance of primates could be predicted by the abundance of food trees or by measures of forest structure. Structural differences such as tree density and size (*Chapter 1*) may influence the ability of arboreal wildlife to travel (Crockett and Eisenberg 1987; Estrada and Coates-Estrada 1996). Capuchins frequently cross openings in the forest by walking on the ground (Freese 1976; Oppenheimer 1982; Chapman et al. 1989a), whereas spider monkeys and howlers are usually found in large trees and rarely come to the ground (Chapman 1988a; Estrada and Coates-Estrada 1996). The influence of food abundance and forest structure and species composition on the densities and group compositions of each monkey species is examined in this study.

METHODS

Study Site

In January of 1996 I chose 13 patches of forest as study sites in Santa Rosa National Park, Costa Rica. Most patches were homogenous in age with the exception of *Cuatro Esquinas* that contained a small ravine of older forest (Table 2-1). Similarly, many fruiting trees, primarily figs, were left alive when *Cerco de Piedra* was a pasture (D. Janzen in Fedigan et al. in press). Close examination of Figure 2-10, page 27, reveals these large residual trees. Forest patch area was calculated by placing a 80m by 80m scale grid onto

a crude vegetation map of the park (Pacheco and Morera 1986). Although patch sizes varied (mean = 35ha, range 22-56, Table 2-1), size did not correlate with forest age ($r = 0.385$, $p = 0.24$). Capuchins, howlers (Mittermeier 1973; Larose 1996; Stoner 1996), and spider monkeys (Fedigan et al. 1988; Chapman 1988b) are known to have home ranges smaller than these patches. All patches were connected to other forest and were not isolated (Fig. 3-1); therefore monkeys had the potential to move into and out of the patches. For a detailed description of Santa Rosa and the study sites refer to *Chapter 2* pages 6-8. In addition to the 13 forest sites I chose a current pasture (Fig. 3-1) as a time-zero data point.

Study Subjects

White-faced capuchins (*Cebus capucinus*) are distributed from Honduras to Columbia (Rodriguez-Luna et al. 1996). Their diet consists of fruits (81%) and insects (17%, Chapman 1987) and occasionally small vertebrates (Chapman and Fedigan 1990). There are approximately 30 capuchin groups in Santa Rosa (Fig. 3-2). Groups are multi-male and rarely subdivide into foraging parties like the other two monkey species; however, groups can be dispersed over a radius of 250m (Chapman 1990b). The literature contains few records of home range size for capuchins; but those that exist are usually less than 100ha (range 32-179ha; Baldwin and Baldwin 1976; Freese 1976; Chapman 1987, Chapman et al. 1988). Some studies suggest that capuchins use their home range similarly in both dry and rainy seasons (Chapman 1988b) but there is evidence that their home ranges may be reduced and centered on water sources in the dry season (Fedigan pers. comm.). I could also find no estimates of home range overlap but it does occur (Chapman and Fedigan 1990). Males disperse on average every 30 months and occasionally remain solitary for some time (Fedigan et al. 1996).

Mantled howling monkeys (*Alouatta palliata*) are distributed from southern Mexico to the west coast of Columbia and Ecuador (Crockett and Eisenberg 1987). Howlers are often considered folivore-frugivores and eat primarily leaves (49%) but opportunistically eat fruit (29%) and flowers (23%, Chapman 1987, 1988a,b; Larose 1996). There are approximately 37 groups of howlers in Santa Rosa National Park (Fig. 3-3). Howlers are

usually associated with very large trees (mean diameter at breast height (dbh) = 62.6cm; Chapman 1988a). Howler groups are multi-male consisting mostly of non-related adults and their offspring (Jones 1980; Clarke and Glander 1984). Home range size of groups can vary greatly between 5 and 108ha (Baldwin and Baldwin 1976; Larose 1996) and can range from no overlap to 100% overlap (Baldwin and Baldwin 1976). Howlers use their home range similarly in the dry and rainy season (Chapman 1988b) but travel less during the dry season (Larose 1996). Juveniles and young adults of both sexes can successfully disperse (Jones 1980; Clarke and Glander 1984). Groups within Santa Rosa often subdivide into foraging parties (Chapman 1990b).

Spider monkeys (*Ateles geoffroyi*) are distributed from Mexico to Panama (Rodriguez-Luna et al. 1996). Their diet is mostly fruit (78%) supplemented with leaves (12%) and flowers (9%, Chapman 1987, 1988a,b). On average spider monkeys use fairly large trees (mean dbh = 43.1cm, range 7-185, Chapman 1990a). Spider moneys live in communities consisting of dynamic, sex-segregated foraging parties (fission-fusion community, Fedigan and Baxter 1984; Chapman 1990a). Female spider monkeys usually forage alone with their offspring and males travel together with low levels of intra-male aggression (Fedigan and Baxter 1984). The home ranges of single spider monkeys vary between 25 and 98ha with males having larger home ranges (81.4ha) than females (54.9ha, Fedigan et al. 1988; Chapman 1990a). There is no evidence that home range sizes for spider monkeys change with season.

Data Collection

I used line transects because they are a systematic, objective, and rapid method to compare population parameters between habitats (Cant 1978; Buckland et al. 1996). Transects are also the most common systematic method to estimate primate densities (Cant 1978; Green 1978, 1982; Freese et al. 1982; Crockett 1982; Branch 1983; Defler and Pintor 1985; Johns 1985b, 1991; Koster and Butynski 1985; Skorupa 1986, 1987; Butynski 1990; Chapman et al. 1988; Weisenseel et al. 1993; Fimbel 1994; Peres in press). Transect density estimates are also sensitive to home range overlap and unused forest areas (Wilson and Wilson 1975a; Cant 1978; Crockett 1982); whereas estimates from

'groups size/home range area' or 'number of monkeys/forest area' are not sensitive to those factors. Lastly, these methods allowed me to sample all three species at the same time and still have the flexibility to analyze each species with their own criteria.

A 600m transect was surveyed within each site at a random compass heading (Fig. 3-1) with the restriction that the transect must remain within the forest patch. Transects were surveyed *ca.* 1 km apart (minimum 600m) so that a single monkey group was unlikely to overlap multiple transects. Other studies have used 1km or $1km^2$ as the distance to distinguish individual groups (Stoner 1996; Fedigan et al. in press). Transects were flagged with orange surveyor's tape at 25m intervals. Global locations (points) were recorded at 50m intervals with Trimble GeoExplorer hand-held GPS units. At least 180 positions were recorded for each point and averaged to give an accuracy of ± 2m for each point. It became apparent from the two-dimensional GPS points that most transects were not exactly 600m long ($\bar{\chi}$ = 558m, SE = 7). I used the two-dimensional transect lengths because forest canopy area, i.e. monkey habitat, varies little with undulations of the forest floor.

Between February and July 1996 each transect was walked once within a two-day cycle to maximize similarity of tree phenologies. Transects were walked in random order and during all daylight hours (0600-1700; Fimbel 1994). I walked along the transects slowly (45min) and stopped every 25m to carefully scan and listen for monkeys. Three assistants helped to increase the sampling effort by 41%. After one month of sampling no monkeys were observed in the three youngest sites; I therefore reduced sample effort in those sites so that effort could be directed to reduce variance in sites where monkeys were observed. From early February to the middle of July, transects with monkeys present were walked on average 95.5 times (range 87-113) and transects without monkeys were walked on average 57 times (51-60). Half of the sampling effort for each site was in the dry season and half in the wet season; therefore monkey densities and food abundances are averaged across seasons.

Chapman et al. (1988) suggested that each transect should be sampled over 100 times before accurate density estimates are reached. Other studies (Cant 1978, Defler & Pintor 1985) suggest that less than 50 samples would produce relatively accurate estimates of

density. These discrepancies are probably due to the encounter rate of monkeys which is a function of transect length, visibility, and the density of animals. I calculated and plotted the percent precision

% Precision = 95% confidence limits / mean number of animals per transect x 100

(National Research Council 1981) of the density estimates for each additional 10 transects walked to verify that the variance in density estimates stabilized by the end of the study (Chapman et al. 1988). Low values of percent precision indicate small differences in estimates from each additional sample.

When a monkey was observed on the transect the following was recorded: date; time; transect; species; horizontal distance to monkey (*r*) using a range finder; location of observer on transect; angle of monkey off transect (θ); sex (for adults); age (dependent infant, juvenile, adult); behavior prior to noticing the observer (feeding, traveling, sleeping); number of monkeys visible; height in tree; height of tree; species of tree; visual estimation of dbh of tree; and if feeding, the part of tree fed on (flower, fruit, young leaves, mature leaves). Each monkey's perpendicular distance from the transect was calculated as the product of *r* and sine θ (Buckland et al. 1996).

In addition to the transect sampling, all groups of capuchins and howlers were followed at least once to determine exact group sizes and compositions. Groups of capuchins and howlers were identified by distinguishing marks and scars of individual members. Three sites had two howler groups; in these sites the different groups were located and counted within one hour to confirm separate groups. Due to the dynamic nature of spider monkey groups no attempt was made to define a group. Group size compositions were adjusted by summing the maximum counts of all age/sex classes (minimum community for spider monkeys, Chapman 1988b). This method is used extensively for spider monkey groups that have fission-fusion communities (Fedigan and Baxter 1984). After comparing the group composition of capuchins with those of other researchers in the park, I realized I was inaccurately distinguishing between male and female adults. Therefore I do not present or analyze sex ratios tor capuchins.

To sample the forest in each site, all stems within 10m of the transect and ≥ 5cm diameter at breast height (dbh) had their dbh measured, height estimated, and were

identified to species. A total of 14.4ha of forest were sampled. About 60 species of plants could be identified in the field; vouchers were collected from trees that were unknown and later identified by park botanists. Nomenclature used in this manuscript is from Janzen and Liesner (1980). More detail in vegetation sampling and analysis methods is provided in *Chapter 2*, pages 8-12.

Density Analysis

Cant (1978) distinguishes three methods for primate density estimation. Group size is divided by the group's home range in *home range mapping*. Group size can be divided by a natural or arbitrarily *delimited area*. Finally, *transect censuses* can be used with an estimate of transect width as the area sampled. I compared my transect density estimates with delimited area densities calculated as group size divided by forest patch area.

Transect methods have the following five assumptions in order of decreasing importance (Buckland et al. 1996):

1. Transects must be randomly located relative to the distribution of monkeys.
2. Monkeys directly on the line are always detected.
3. Monkeys are detected at their initial location, prior to any movement in response to the observer. Animal movement after detection is not a problem.
4. Accurate distances are recorded. In the current study a range finder was used with an accuracy of +/- 10cm at a distance of 15m.
5. Observations are independent events.

Assumption 5 requires that cohesive groups should be counted as clusters rather multiple individuals (Buckland et al. 1996). However, the estimation of group density relies strongly on determining the distance of the middle of the group from the transect. In the current study, especially with capuchins and spider monkeys, individuals were highly dispersed within a group. Chapman (1990b) found that capuchin groups could be dispersed over a radius of 250m (see also Freese 1976). In order to analyze densities as group units rather than individuals, group size must be accurately known for groups that are directly on the transect (Buckland et al. 1996); however, I recorded many cases in which the group was probably directly on the transect but not all individuals (peripherals)

were within visual distance. Failure of assumption 5 has little to no effect on density but underestimates variance (Buckland et al. 1996); it does not incorporate the variance in the calculation of average cluster size. If Assumption 1 is met and a robust estimator of variance is used, Assumption 5 can be ignored (Buckland et al. 1996). For the above reasons the densities were analyzed as individual density rather than group density (see also Green 1978; Cant 1982; Freese et al. 1982; Chapman et al. 1988; Johns 1991; Weisenseel et al. 1993; Peres in press).

Monkey densities were calculated using the program DISTANCE (Laake et al. 1996). DISTANCE calculates the density of monkeys from the equation

$$D = n / A$$

where D is the density of monkeys, n is the total number of monkeys observed for all walks of the transect, and A is the area sampled. The area sampled was calculated from

$$A = 2 L \mu$$

where L is the total distance walked (length of the transect multiplied by the number times the transect was walked), and μ is the effective strip width. These formulas result in the same estimate as averaging the density estimate from each walking of the transect. μ is calculated from the area under a plotted curve of the probability of detection, g(y), vs. the perpendicular distance from the transect (y; Fig. 3-4). For example, g(39) is the probability of detecting a monkey 39m from the transect. In Figure 3-4, g(25.5) is 0.30, meaning 70% of the monkeys 25.5m from the transect are missed. The area under the curve (μ) in Figure 3-4 is 19.8m, meaning the distance one can detect monkeys effectively is 19.8m. In addition to the density estimate, DISTANCE analyzes the proportion of density variance contributed by monkey encounter rates and the estimation of μ. Early studies on primates estimated μ using a variety of methods that were either less objective or without statistical rationale (Wilson and Wilson 1975a; Green 1978; Freese et al. 1982; Branch 1983; Defler and Pintor 1985, Chapman et al. 1988; Brockelman 1980; Butynski 1990).

Several types of curves can be used to estimate g(y). Each model contains a key function and a series expansion; the series expansion adjusts the key function to improve the fit of the model. Uniform, Half-normal, and Hazard-Rate models are the most

recommended key functions based on their robustness and estimator efficiency (Buckland et al. 1996). Series expansions, such as cosine, simple polynomial, and Hermite polynomial, are composed of one or more parameters (*a*). More parameters reduce the bias of the density estimate but increase the estimate's variance (Buckland et al. 1996). Originally I allowed DISTANCE to select the best fit and most parsimonious model based on evaluations using Akaike's Information Criterion (Laake et al. 1996); however, the Hazard Rate key function was selected for 8 of the 28 species-site combinations which produced unrealistic estimates of μ (e.g. 3.97m). Peres (in press) had to pool data from multiple sites to get reliable μ estimates from the Hazard Rate model. The Uniform key function was selected for all other species-site combinations; therefore I limited DISTANCE to the Uniform key function for more realistic μ estimates (Table 3-1). The Uniform key function with a cosine series expansion (together called the Fourier Series) has the equation

$$g(y) = \frac{\mu}{w}\left(1 + \sum_{j=1}^{m} a_j \cos\left(\frac{j\pi y}{w}\right)\right)$$

where y is the perpendicular distance, w is the truncation point (y_{max}), and j is the number of parameters (a) in the series expansion. Koster and Butynski (1985) found that the Fourier Series detection function was the most accurate and robust for four primate species.

After the above modifications, three estimates of μ still appeared low; 9m for capuchins in *Cerco de Piedra*, 5m for howlers in *Laguna*, and 10m for spider monkeys in *Mirador de Naranjo*. The underestimates of μ for the howler and spider monkeys are predictable due to the small number of monkey sightings; 9 and 4 respectively. It is unclear why the 61 capuchin sightings produced an underestimated μ. This monkey group is the only group in this study that is habituated to humans. The capuchins probably did not alarm call towards humans as much as other capuchin groups which would reduce the chances of observers seeing the monkeys at maximum distances. For these three species-site combinations μ was used from other species within the site that had the maximum number of sightings; 15.4m from howlers in *Cerco de Piedra*, 28m from capuchins in *Laguna*, and 21.8m from howlers in *Mirador de Naranjo* (Table 3-1). This is acceptable

if it is safe to assume that all three species of monkeys have similar detection functions of distance (visibility; Buckland et al. 1996). Site explained more variation in μ ($F_{6,12}$ = 1.737, p = 0.196) than species ($F_{2,12}$ = 0.065, p = 0.937) in sites where all three species co-occurred, but neither explained significant variation.

Truncating the farthest sightings often improves the variance in density estimates by removing outliers and improving the fit of the model (Buckland et al. 1996; Laake et al. 1996). The farthest observations provide relatively little information about density (Buckland et al. 1996); therefore five percent of the most distant monkey sightings were not used to estimate μ (truncated), as recommended by Buckland et al. (1996).

In the present study I did not analyze densities separately for the dry and rainy season. Transect sampling was balanced between the seasons and I present these density estimates as an average of the two seasons. Further analyses may indicate differences between the seasons.

Food Abundance

One recent method to estimate habitat-wide fruit abundance for primates was based on tree diameters at breast height (dbh, Chapman and Fedigan 1990; Chapman et al. 1992, 1994; Malenky et al. 1993). The dbh of trees of food species have been summed as a relative estimate of fruit abundance (Chapman 1988a,b, 1990a,b; Chapman et al. 1994). This method assumes that fruit abundance is linearly correlated with dbh, and has not been applied to estimate leaf abundance. I propose a new method for calculating food biomass from dbh using published allometric relationships; fruit (Peters et al 1988; Niklas 1993, 1994) and leaf biomass (Kittredge 1944; Kira and Shidei 1967; Attiwill and Ovington 1968; Whittaker and Woodwell 1968; Negi et al. 1983; Clough and Scott 1989; Singh and Yadava 1991) are known to be power functions of dbh. Furthermore, studies of tropical trees have shown that single regressions can accurately explain fruit and leaf biomass for several tree species combined (Kira and Shidei 1967; Ogawa and Kira 1977; Peters et al 1988).

Food biomass was calculated using published allometric relationships between dbh and biomass of food items

$Fr = 47dbh^{1.9}$ ($R^2 = 0.78$, Peters et al. 1988; similar to Niklas 1993)

$L = 38.4dbh^{1.65}$ (derived from equations in Whittaker and Woodwell 1968)

where Fr is the mass of fruit (grams), L is the mass of leaves, and dbh is measured in centimeters. Food biomass was the sum of fruit and leaf biomass for each site.

Peters et al. (1988) formulated the fruit biomass equation on genera also found in Santa Rosa: 2 *Ficus* spp., *Albizia*, *Coccoloba*, 2 *Cordia* spp., *Annona*, and *Psidium guajava*. The fruit equation also explains biomass for *Stemmadenia* (McDiarmid et al. 1977; Peters et al. 1988). I only included adult trees (>10cm dbh) in fruit biomass estimates. Assuming a 1:1 sex ratio (see Bawa and Opler 1975; Glander 1975), half of the calculated fruit biomass was included from dioecious species (*Bursera simaruba*, *Cecropia peltata*; *Chlorophora tinctoria*, *Sciadodendron excelsum*, *Simaruba glauca*, *Spondias mombin*, Bawa and Opler 1975; Croat 1978; Glander 1975, 1978). Peters et al. (1988) based their formula on 2 monoecious fig species so I did not correct fruit biomass for monoecious species. *Brosimum alicastrum* is a sequential hermaphrodite; therefore fruit biomass was only included for trees <70cm dbh (see Peters 1991). In addition, only trees greater than 20cm dbh were included in the howler diet because howlers rarely (<0.02% of forage time) forage in smaller trees (Leighton and Leighton 1982; Chapman 1990b; Larose 1996, and pers. comm.). Capuchins and spider monkeys frequently used trees <20cm dbh (34.6% and 25% respectively, Chapman 1990b). Although there is one report of capuchins eating fig leaves (2.4% of feeding time, Chapman 1987) it is a rare behavior (C. Goforth pers. comm.); therefore leaf biomass was not included in the food biomass estimate for capuchins.

The allometric relationship for flower biomass is not well documented in the literature for trees (shrubs studied by Midgley and Bond 1989, and Le Maitre and Midgley 1991); therefore flower biomass was left out of the food biomass estimate. The weight of flowers is relatively insignificant compared to fruits and leaves and therefore would probably have little impact on food biomass estimates.

The estimate of food biomass was summed for food species of each monkey species within each site. Food lists for each monkey species (Table 3-2) were derived from diet studies in Guanacaste where the percent of total diet was presented (Freese 1977; Glander

1975, 1978; Chapman 1987; Chapman and Fedigan 1990; Larose 1996). I originally calculated food biomass for tree species that constituted at least 1% of the diet (Table 3-2) however I became concerned that species with low representation in the diet (1-2%) were being given too much weight in the food biomass estimate. I therefore used food items that constituted at least 2% of the diet. All food items included were confirmed to be available during the study period by personal observation or consultation with other monkey researchers in the park at the time (L. Rose and C. Goforth).

There are several shortcomings to using this method to estimate food abundance and availability. This method fails to account for the proportion of trees of a given species that fruit, and the proportion of biomass eaten by competitors. Wheelwright (1986) found that many species of Costa Rican trees had high year-to-year variance in fruit production. Many of the trees sampled may not have been accessible to monkeys, i.e. isolated canopy. Likewise, fruits fallen to the ground can account for a considerable amount of the fruit produced (Leighton and Leighton 1982) and would not be available to monkeys.

Food biomass may also correlate poorly with available energy or nutrients. Most estimators of food abundance assume that all food resources (e.g. fruit vs. leaves) are of equal value to the consumer (Malenky et al. 1993). Large proportions of the fruit mass may consist of inedible parts such as husks and pits; likewise, young leaves are much more preferred by howlers because of lower amounts of secondary compounds and more nutrients (Estrada 1984). Leaves of early successional trees may be more palatable and have lower chemical defenses than later successional tree species (Cates and Orians 1975; Opler 1978; Ewel 1980). However, the benefits of using this method are: 1) it allows easy comparison between study areas, 2) dbh is easily measured; and 3) it allows food abundance to be calculated separately for each study species.

Insect biomass constitutes a large proportion of capuchin monkey diet (17% of foraging time, Chapman 1987) but insect biomass was not estimated in this study's food biomass estimate. Capuchin food biomass was therefore underestimated in each study site.

Statistics

To examine the change in monkey densities with forest regeneration, monkey densities were plotted against forest age and Axes 1 site scores (A1, regeneration variable) from the DCA (*Chapter 2*). I used a regression to test whether or not monkey densities increase linearly with food biomass. I also plotted and regressed food biomass against forest age to examine how food resources changed with forest regeneration. Multiple regressions were used to test the dependence of monkey density on environmental variables: A1 (regeneration variable, *Chapter 2*), A2, food biomass, tree density, tree basal area, and tree species diversity. Forest age was removed from the regressions since diagnostics for collinearity (tolerance) indicated that it might cause instability in the regressions (SPSS Inc. 1997). This was probably because A1 was also in the model. Likewise, I had originally hoped to include the percent of trees with evergreen leaves and the percent of trees with animal dispersed fruit; however these were already linearly correlated with forest age (*Chapter 2*) and I wanted to minimize intercorrelation (Zar 1984). Multiple regressions were calculated using forward selection of independent variables. Forward selection is a stepwise procedure where the independent variable with the highest correlation coefficient is included in the model first, and then each variable is entered sequentially in decreasing order of correlation coefficient only if it meet the entry criteria ($p < 0.05$; SPSS Inc. 1997).

To study the influence of forest regeneration on monkey group composition, multiple regressions were used to test the dependence of sex ratios, age ratios, and group sizes on environmental variables: A1 (regeneration variable, *Chapter 2*), A2, food biomass, tree density, tree basal area, tree species diversity, and monkey density. Group size was also included as a variable in the multiple regressions to explain variation in age and sex ratios. I used the average size and composition of groups for sites with two howler groups. Although the ratio of immature:adult females or infants:adult females are commonly used as indexes of population viability, some studies have shown a more conservative ratio may provide a better index (Heltne et al. 1976). I used the proportion of immatures (juveniles + infants) to adults as the age ratio; however I also present the immature:adult female ratio in tables for howlers and spider monkeys for comparisons with other studies.

In regression analysis it is assumed that for each value of the independent variable (x) there is a normal distribution of the dependent variable (y, Zar 1984). Since I did not have more than two sites of the same age (or other independent variables) I could not test for normality in the dependent variables. Age and sex ratios were arcsine transformed to improve the normality of proportional data (Zar 1984). Heteroscedasticity was apparent in some regressions (i.e. increase in variance of residuals with increasing *X*); in those cases logarithmic transformations of the dependent variable were used (Zar 1984).

RESULTS

Monkey Density and Food Abundance

The percent precision and density leveled-off for all site/species combinations by the end of the study (e.g. Figure 3-5). This implies that further sampling would not have reduced the variation in density estimates. Most of the variation in density estimates (57.6-100% of variance) was due to variable encounter rates rather than the estimation of μ (0-42.4%). In other words, the average number of monkeys that were seen each time the transect was walked introduced the most variation to the density estimate (see #2 in Appendix 3).

Monkey densities were positively correlated with the regeneration of tropical dry forest. The density of capuchins increased linearly with forest age ($R^2 = 0.598$, $p = 0.001$, Fig. 3-6) and A1 from the DCA in *Chapter 2* ($R^2 = 0.592$, $p = 0.001$). Residual fruiting trees in *Cerco de Piedra* may have caused higher capuchin densities than the other 40-year-old forest, *Laguna Escondida*. The densities of capuchins did not appear to level off within the chronosequence of sites although the two undisturbed sites had similar high densities (Fig. 3-6).

Howler density had a significant positive linear relationship with forest age ($R^2 = 0.396$, p = 0.016, Fig. 3-7) and A1 ($R^2 = 0.428$, $p = 0.011$); however the plot (Fig. 3-7) suggested a more complex relationship. Residual fruiting trees in *Cerco de Piedra* may have inflated howler densities. In addition, 90% of the howler sightings in *Cuatro Esquinas* were within two areas of older age (70-90 years old). If these two sites are

considered anomalies, the density of howlers peaks at 81/km^2 around 100 years of forest regeneration, and then drops to 33/km^2 in the oldest forest.

Spider monkey densities were significantly related to forest age (linear regression, R^2 = 0.54, p = 0.00261, Fig. 3-8) and A1 (R^2 = 0.365, p = 0.022); however, the plot of density vs. forest age indicates a non-linear relationship. Spider monkey densities were high in the two pristine forests (46 and 67/km^2) but very low in all other sites.

Although monkey densities were related to forest age, a more proximate reason, such as food abundance, is more likely the causal influence on monkey density. Capuchin (Fig. 3-9, R^2 = 0.742, p = 0.000076), howler (Fig. 3-10, R^2 = 0.667, p = 0.00036) and spider monkey densities (Fig. 3-11, R^2 = 0.334, p = 0.0304) were all linearly and positively related to food biomass estimates. Howler densities are more strongly related to leaf biomass (R^2 = 0.689, p = 0.000238) than to fruit biomass (R^2 = 0.592, p = 0.001) as one would predict from their relative proportions in howler diet. High capuchin and howler densities in *Cerco de Piedra* are now explained by food biomass. On the other hand, food abundance did not explain the high density of howlers in *Cuatro Esquinas*. The small area of older forest in *Cuatro Esquinas* did not greatly increase the site's overall food biomass estimate. Spider monkey densities were significantly correlated with fruit biomass (R^2 = 0.328, p = 0.032) but not leaf biomass (R^2 = 0.101, p = 0.268).

To examine when food biomass reaches maximum levels during regeneration, food biomass was regressed against forest age. Food biomass for capuchin (Fig. 3-12, R^2 = 0.441, p = 0.00961), howler (Fig. 3-13, R^2 = 0.548, p = 0.00247), and spider monkeys (Fig. 3-14, R^2 = 0.747, p = 0.000068) increased linearly with the age of the forest. Clearly, the food biomass estimate for *Cerco de Piedra* is higher than the other 40-year-old forest, *Laguna Escondida*.

Multiple regressions of monkey densities versus A1, A2, food biomass, basal area, tree density, and tree species diversity were used to examine the combined influence of environmental variables. Capuchin ($F_{1,11}$ = 28.18, p = 0.0002) and howler densities ($F_{1,11}$ = 19.368, p = 0.001) were only associated with higher food biomass. Spider monkey densities increased with forest regeneration (A1), and decreased with tree diversity ($F_{2,10}$ = 10.593, p = 0.003).

Initially the monkey densities produced by DISTANCE may appear unrealistically high; however, DISTANCE estimates were significantly correlated with density estimates using delimited area methods ($p \leq 0.008$, $R^2 \geq 0.460$, Fig 3-15). To calculate delimited area densities, known group sizes (Tables 3-3 and 3-4; community size for spider monkeys, Table 3-5) were divided by the area of the forest patches. Most DISTANCE densities were lower than the delimited area densities: 82% of capuchin densities, 78% of howler densities, and 89% of spider monkey densities.

Group Composition

A multiple regression of the environmental variables and age ratio was calculated for each species. Capuchin age ratios were positively related with forest regeneration (A1) and tree density ($F_{2,7} = 12.006$, $p = 0.005$, Table 3-3). Howler age ratios were positively related with tree basal area ($F_{1,7} = 10.828$, $p = 0.013$, Table 3-4). Both basal area and food biomass are both power functions of dbh; therefore I suspected that howler age ratios might be related to food biomass. The regression was not significant ($R^2 = 0.258$, $p = 0.136$) but the 4 sites with the lowest food abundance had significantly lower age ratios (mean = 0.34±0.08SD) than the 5 other sites (0.60±0.08SD; $t_{(2),\,7} = 4.728$, $p = 0.002$). There was also a significant difference in immature:adult female ratio between low (0.48±0.13SD) and high food abundance (0.80±0.19SD; $t_{(2),\,7} = 2.894$; $p = 0.023$). No environmental variables were significant in explaining age ratios for spider monkey communities (Table 3-5).

Male:female sex ratio for howler groups (Table 3-4) and spider monkey communities (Table 3-5) were not significantly related to any environmental factor.

Capuchin group size (Table 3-3), average howler group size (Table 3-4), spider monkey community size, and the average size of spider monkey foraging parties (Table 3-5), were not explained by any of the variables in the multiple regressions. Appendix 2 lists the specific compositions of all groups for the three species as I determined them in 1996.

DISCUSSION

Transect Methodology

There are several drawbacks to using transect methods. The accuracy of the estimate is highly dependent on the estimate of transect width (μ), on the accuracy of distance measurements, and on the interest of the observer. For example, if μ in increased by 5m the density estimate for spider monkeys in *Bosque Humedo* is reduced from 67 to 49/km^2. Whether or not the density estimate is representative of a larger area also depends on how much of the study area is sampled by the transect. A 600m x 50m transect only samples 9% of a 35ha forest patch. Lastly, a great deal of time is needed to survey and clear trails for permanent transects (1 person-month for 13 transects of 600m).

On the other hand there are many benefits to using transects rather than other density methods. The most important benefit is that transects provide a rigorous and objective method to compare the relative abundance of multiple species in a variety of habitats. When compared to other density estimate methods, one does not need to follow and determine home range areas and areas of home range overlap for each study group (31 groups in the present study) to calculate densities using the home range method. More importantly, one does not need to follow groups to determine which areas are *not* being used by monkeys to correct delimited area densities. Transects also provide a convenient method to collect data on habitat characteristics that are directly applicable to the density estimate. By sampling both monkeys and trees with the same transect I sampled trees (20m x 600m) in 36-46% of the area sampled for monkeys (50m x 600m). This allows for a much more powerful correlation of monkey densities with tree data than would a square vegetation plot of equal area within a large home range. Transects are also more likely to encompass a wider range of natural variation within habitats than a square plot of equal area.

Transect methods are probably the only realistic method to estimate spider monkey density (Cant 1978). With respect to the home range method of density estimation, neither the numerator (number of monkeys) nor the denominator (area) can be clearly defined with spider monkeys because group composition is highly dynamic (Cant 1982).

Unfortunately, in wild populations there rarely are 'true' or 'accurate' densities to compare with any method. Unless monkeys spend all of their time uniformly over all of the study area, different methods will result in different estimates. Skorupa (1987) found that transect methods have equal probabilities of over- (8-50%) or underestimating (7-46%) densities compared to home range methods. Density estimates can really only be compared when they are derived from similar methods (Wilson and Wilson 1975a). Transect methodology and density theory is discussed in greater detail in Appendix 3.

Density Estimates

Fedigan et al. (1996; in press) calculated ecological densities from total abundance in the park divided by the area of suitable habitat (evergreen and mixed deciduous forest). Their results suggest overall ecological densities of 7.5/km^2 for capuchins and 7.9/km^2 for howlers in Santa Rosa in 1992. Other studies have found much higher densities within smaller areas of the park using home range methods (19.2-91.8 howlers/km^2, Larose 1996) and transect methods (19-33 capuchins/km^2 and 19-28 howlers/km^2, Chapman et al. 1988; 61±14 capuchins/km^2 and 85±19 howlers/km^2, maximum in current study). Chapman et al. (1988) emphasized that their study area was not representative of the park and that their densities should not be extrapolated to the forested area of the park. I agree and suggest two explanations for the discrepancies between the overall park density (Fedigan et al. 1996, in press) and higher density estimates.

Firstly, density estimates from isolated forest patches will not be similar to estimates from an area within continuous forest (Cant 1978). Secondly, the problem with the delimited area method is that it does not account for home range overlap or unused areas (Cant 1978). Many studies have shown high densities in forest patches (103 howlers/km^2 in La Pacifica, Guanacaste, Clarke and Zucker 1994; 1040 howlers/km^2 in Panama, Baldwin and Baldwin 1976) or a crowding effect of groups following forest fragmentation (Lovejoy et al. 1986). The lower plateau is much less fragmented (Fig 3-1) and may have lower monkey densities (Table 3-6) due to less home range overlap and more unused areas (Fedigan et al. 1985). Figures 3-2 and 3-3 suggest that a large proportion of the forest in the lower plateau is not being used by the known monkey groups. Like Chapman

et al. (1988), I would not recommend applying the presented densities to larger tracts of continuous forest, nor should the densities be applied to forest fragments without specific forest age or food abundance estimates.

In the past it has been very difficult to estimate the number of solitary monkeys within the park because censuses are not designed to distinguish between solitary individuals (Fedigan et al. 1985, 1996, in press). By dividing the number of solitary monkey sightings by the total number of monkey sightings, my results suggest that 1.7% of capuchins, 1.2% of howlers, and 2.0% of spider monkeys are solitary, which are similar to estimates in the literature (Capuchins, 1%, Fedigan et al. 1985; Howlers, 5%, Estrada 1982; 3% Fedigan et al. 1985; 0.8%, Clarke and Zucker 1994, 6-7%, Fedigan et al. in press; Spider monkeys, 1.6%, Chapman 1990a).

Capuchins

Capuchin densities were linearly correlated with both forest age and food biomass. The densities did not level off within the first 100 years of forest regeneration; however the two undisturbed sites had similar high densities (59-61/km^2). Although, the capuchin density in the undisturbed forest is high, it is within the range of reported densities for the species (maximum 68-94/km^2, Baldwin and Baldwin 1976). The late successional forest of Barro Colorado Island, Panama, has a capuchin density of 33/km^2 (Oppenheimer 1982), similar to the range of densities in 50-100 year old forests of the current study.

The densities appeared to be more related to food biomass than forest age. The third highest density of capuchins was in *Cerco de Piedra* which suggests that density can be artificially raised in younger forest by leaving residual fruiting trees in abandoned pastures. Fedigan et al. (1996) suggested that capuchin groups may increase their size and home range into the regenerating forest as it becomes profitable, but must maintain access to the higher fruit abundance (see *Chapter 1*) and abundance of water hole cavities in trees of older forests (Fedigan et al. 1996). Although this could be interpreted from the current results, it appears more likely that capuchins are able to exist at variable densities depending on food abundance in the habitat.

Capuchin age ratio was related to forest regeneration (A1) and tree density. Although the age ratio was not explained by food biomass (perhaps due to intercorrelation), the proportion of immature capuchins is higher in older forests where there is more food. This would be predicted if female reproductive success was a function of food abundance. Fedigan et al. (1996) found that birth rates were positively correlated with the amount of early rainfall the previous year. This is consistent with my results if rainfall is an index of food abundance, which has been assumed in the past (Fedigan et al. 1996; Chapman et al. 1989b).

The latest age ratios for the park (0.89 in 1992, Fedigan et al. 1996) suggest that the ratio has increased over the past 25 years (0.49 in 1972, Freese 1976) which is consistent with a correlation between the age ratio and forest age. Heltne and Thorington (1976) compared the Santa Rosa age ratio to BCI (1.83, Oppenheimer 1968, 1982) and suggested that the capuchins in Santa Rosa may have been in a depressed state. Only the oldest forest had a balanced age ratio (1.00), suggesting a viable group composition (Heltne and Thorington 1976). These results suggest that the population may have had low age ratios but that the ratio is increasing as the park regenerates.

Although sex ratios for capuchins could not be analyzed, results from Fedigan et al. (1996) suggest that the male:female sex ratio is also increasing as the forest regenerates. Currently, the male:female sex ratio of capuchins at birth is 3:1 (n=40, Fedigan et al. 1996). If a low male:female sex ratio is an indicator of a stressed population (Heltne et al. 1976), it appears that the capuchin population is becoming less stressed as the forest regenerates.

Capuchin group size was not explained by any of the habitat variables included in the multiple regression. Oppenheimer (1982) suggests that the size of capuchin groups is related to age structure rather than habitat variables, and that group fissioning may be related to the proportion of old females in the group.

Howling Monkeys

Several studies suggest that howlers prefer older, more evergreen forest rather than younger, more deciduous forest (Freese 1976; Heltne et al. 1976; Chapman et al. 1989a;

Chapman and Balcomb in press). The percent of evergreen trees increased linearly with the age of the forest (Chapter 2), yet the highest howler densities were not in the forest with the most evergreen trees (*Quebrada Puercos*). Similarly, *Cerco de Piedra* had a low proportion of evergreen trees but high howler density. The above results suggest that deciduous/evergreen distinctions of habitat may be inadequate to define optimal habitat for howlers.

The densities of howlers increased with forest age but there is some indication that density decreased as the forest reached maturity. This could be explained by a lot of tree falls and canopy gaps in the oldest forests that may have reduced food abundance and the ability to travel through the canopy. The current results indicate that *ca.* 60 years of natural regeneration is required before howler densities are similar to undisturbed areas; however a better predictor of howler density within Santa Rosa is food abundance.

Early studies suggested that the densities of howlers are not limited by food resources and their home ranges include more food than groups could ever eat (Chivers 1969; see Baldwin and Baldwin 1976; Coelho et al. 1976). However, Glander (1975; 1978) and Jones (1980) suggested that not all leaves and fruit are palatable between and within tree species and that the apparent abundance of food may be offset by a lack of nutrients or the presence of secondary compounds. My results suggest that when the preferred diet items are recognized, howler densities are strongly related to food abundance (see also Stoner 1996).

The range of howler densities in the neotropics is large, 0.8-180/km^2, with an average of 50/km^2 (Chapman and Balcomb in press; Peres in press). Extremely high densities can occur when howlers are crowded into forest patches (1040/km^2, Baldwin and Baldwin 1976) and low densities of *Alouatta* spp. can occur in large tracts of continuous primary forest (12/km^2, Peres in press). Peres (in press) found that densities of *Alouatta* spp. in the neotropics show strong positive associations with forests with heterogeneic canopies (canopy gaps, edges, and high species diversity). Howlers may be able to benefit from the higher productivity and abundance of young leaves (howlers' preferred food item) near forest edges (Peres in press). This is consistent with the higher howler densities for the upper plateau than the lower plateau of Santa Rosa.

The proportion of immature howlers increased with the structure of the forest (tree basal area) and was higher in sites with higher food abundance. This is consistent with the increase in the proportion of infants within the entire park as the park regenerates (Fedigan et al. in press). Clarke and Zucker (1994) suggest that an immature:adult female ratio of 0.5 is sufficient to maintain stable howler populations. Using 0.5 as the benchmark, groups in sites with low food abundance appear to be stable (0.48±0.13); whereas groups with high food abundance may be growing in size (0.80±0.19).

Carpenter (1962) suggested that a low male:female sex ratio may indicate a recent decrease in population size. Howler sex ratios in the current study were not related to any of the environmental variables tested, but the average for all study groups (0.43) was within the range presented in the literature (min.=0.31, La Pacifica, Guanacaste, Clarke et al. 1986; max=0.82, La Selva, Costa Rica, Stoner 1994).

There is some evidence that larger howler groups occur in areas of higher food abundance, potentially due to higher reproductive success and lower levels of intragroup competition for food (Gaulin et al. 1980; Chapman and Balcomb in press). In the present study, howler group size was not explained by any of the environmental variables including forest regeneration, food abundance, and howler density. Crockett (1996) suggested that group size is more a function of group age and population growth than food availability. Recently formed groups start small, increase with density, and then level off or fragment as density continues to increase (Chivers 1969; Crockett 1996). Groups may also be able to divide into temporary foraging parties to adjust to the food abundance and distribution within habitats (Chapman 1990b) which would not be detected in the current study.

Spider Monkeys

The upper limits of primate density, but not the lower limits, are set by the food abundance of primate habitats (Butynski 1990). This appeared particularly true for spider monkeys. Densities were positively correlated with food abundance; however, some sites with high food abundance had very low spider monkey densities. Coelho et al. (1976) suggested that spider monkey densities are magnitudes lower than the carrying capacity in

Tikal, Guatemala, based on food abundance and bioenergetic estimates. Densities of spider monkeys may lag far behind the carrying capacity of the habitat due to slow population growth.

An alternative hypothesis is that spider monkey densities are still influenced by hunting pressure that occurred over 25 years ago. Hunting pressure may have been lower in the undisturbed forests than the rest of the park, which would explain the large difference in current densities. Many studies have suggested that historical hunting pressure strongly influences *Ateles* densities (Freese et al. 1982; Chapman et al. 1989a).

Spider monkeys have been observed in regenerating forest only 20 years old and 4m tall (Chapman et al. 1989a; Fedigan et al. 1996). This led Chapman et al. (1989a) to suggest that with protection from hunting, spider monkeys have the ability to quickly colonize and "flourish" in regenerating habitats. The current study agrees that spider monkeys are occasionally seen in young forest, but the densities of spider monkeys after 25 years of protection from hunting are very low in forests less than 100 years old. I suspect that the density of spider monkeys in the 20-year-old forest reflects monkey travel between older forests north and south of the site. Further evidence that the group did not spend all of its time in the site was that the group size/forest area density estimate was five times higher than the DISTANCE estimate. Studies on *Ateles paniscus* have shown that they are able to use, but do not live entirely within, adjacent disturbed forest (Johns and Skorupa 1987).

Unfortunately few published densities for *A. geoffroyi* are available to compare with the current results. Chapman (1988b) found that approximately 42 spider monkeys ranged over 147ha with a density of 29/km^2. Coelho et al. (1976) found spider monkey densities of 45/km^2 in their Tikal study site; however, only half of the study site was used by the monkeys resulting in an ecological density of 90/km^2. These reports suggest that my density estimates in the park are within the natural range for spider monkeys.

None of the environmental variables including food abundance and monkey density explained the variance in the size or composition of spider monkey communities, nor the size of foraging parties. This could be due to the highly dynamic nature of spider monkey group composition. Spider monkey groups are known to fuse and separate at relatively

short intervals (Chapman 1988b, 1990a) and males often associate separately from females (Fedigan and Baxter 1984), adding to variance group composition. Furthermore, smaller groups have higher variance from the expected or optimal group composition (Altmann and Altmann 1979).

The age ratios of spider monkeys in Santa Rosa indicate that they may be in a depressed state when compared to other neotropical sites (Heltne and Thorington 1976). Age ratios were highly variable between sites and did not vary with habitat variables, but those from undisturbed sites (0.22-0.79) and the average (0.57) were below ratios from Tikal, Guatemala (1.00-1.08, Coelho et al. 1976, Cant 1978). The average ratio of immature:adult female (mean = 0.83) is also lower than the ratio in Tikal (1.54-1.57, Coelho et al. 1976, Cant 1978). This suggests that the population in Santa Rosa may have higher immature mortality or lower reproduction than Tikal. On the other hand, the age ratio in Santa Rosa was only 0.33 (immature:female = 0.56) in 1972 suggesting that the age ratio is slowly recovering from disturbance.

Chapman (1989b) suggested that the proportion of females in a population was positively related to the productivity (annual rainfall) of the habitats within Guanacaste, and also within the neotropics. The sex ratios of spider monkeys in the present study (mean = 0.55) are slightly lower than the earliest re ports (0.67, Freese 1976) but are similar to the those in Tikal (0.45-0.57, Coelho et al. 1976, Cant 1978). My results do not support conclusions that Santa Rosa has a low proportion of males (0.18, Chapman et al 1989b) and suggest that the male:female sex ratio is within the normal range for the species.

Chapman (1988b) estimated a community of 42 spider monkeys whose range (147ha) included *Bosque Humedo*. My estimate of 11 individuals is therefore probably not the entire community but could relate to the number of individuals that strictly use *Bosque Humedo*, rather than the entire community. This illustrates the difficulty in using community size, rather than foraging party size, as a population parameter.

Chapman (1990b) found that the size of foraging parties could be predicted by the distribution and density of food trees within a habitat. When food trees were "scarce" and far apart the spider monkeys traveled in small foraging parties, apparently to minimize the

costs of a large group travelling long distances for little food. It may be that the size of foraging parties correlates with food abundance on a smaller scale than an entire forest patch. The average foraging party size in the present study (mean = 4.24±2.49SD) is similar to previously published averages (4.94±4.18SD, Chapman 1990a).

Interspecific Comparisons

The stronger relationship between monkey density and food abundance for capuchins (R^2 = 0.742) than for howlers (R^2 = 0.667) and spider monkeys (R^2 = 0.334) suggests three possibilities. Firstly, a factor other than food abundance may influence howler and spider monkey densities more than it may capuchin densities. Secondly, I may have calculated a better estimate of food abundance for capuchins than for howlers or spider monkeys. The fact that howler and spider monkey diets consist of both leaves and fruit may complicate food abundance or availability estimates. For example, 1kg of fruit is probably 'worth' more to the monkeys than 1kg of leaves.

On the other hand, the stronger relationship may suggest that capuchin densities are able to respond more quickly to temporal variation in the carrying capacity of a habitat than howlers or spider monkeys. Capuchins do have a higher maximum rate of increase (r_{max}=0.16) than howlers (0.15) or spider monkeys (0.10, Robinson and Redford 1986, see also Fedigan and Rose 1995). Many studies suggest that body size, proportion of fruit and flowers in diet, dietary specialization, home range size, and a slow reproductive rate are negatively related to the ability of a species to survive in disturbed forests (Freese 1976; Freese et al. 1982; Johns 1985a, 1992; Skorupa 1986; Johns and Skorupa 1987; Chapman et al. 1989a; Bearder 1991). Similarly, insectivorous species may benefit from secondary forests (Freese 1976; Lovejoy et al. 1986; Schwarzkopf and Rylands 1989). Based on these generalizations the order of species returning to a regenerating forest following disturbance should be capuchins, howlers, and spider monkeys.

Capuchins returned first to the abandoned pastures after *ca.* 20 years of regeneration. The range of regeneration stages used by capuchins is consistent with suggestions that capuchins are able to use a wide range of habitats (Freese 1976; Chapman et al. 1989a). After *ca.* 40 years of regeneration, male/female howler pairs colonized the abandoned

pastures (see also Fedigan et al. in press). Only after 50 years of regeneration did spider monkeys begin to use abandoned pastures. Unlike capuchins and howlers, spider monkeys did not inhabit *Cerco de Piedra* even with its high food abundance. In the past, individual spider monkeys have lived within *Cerco de Piedra* but they disappear after a short time (Fedigan pers. comm.). Branch (1983) also found that *Ateles paniscus* and *Ateles belzebuth* were only found in primary forest, *Alouatta belzebul* were found in all areas with "reasonably" tall forest including secondary and selectively logged forest, while *Cebus apella* was found in the widest range of habitats. These results support predictions based on diet, reproductive rates, and body size with respect to relative habitat tolerance.

Studies have suggested that folivorous species have higher population densities and smaller home ranges than folivore-frugivores or frugivore-insectivores, possibly due to more abundant and evenly distributed food sources, (Eisenberg and Thorington 1973; Clutton-Brock and Harvey 1979; Freese et al. 1982). Freese et al. (1982) also note that within the literature, *Alouatta* usually have higher densities/biomass than *Ateles* within study areas. Although the current density estimates have large associated variance, they agree with these predictions; the decreasing order of maximum densities were howlers (85/km^2 ±19SE), spider monkeys (67/km^2 ±17), and capuchins (61/km^2 ±14).

Other Determinants of Population Density and Composition

Although this study demonstrates that forest regeneration and habitat quality can have an effect on primate populations; other factors such as pesticides (Baldwin and Baldwin 1976; Heltne et al. 1976), hunting pressure (Peres in press), disease (Carpenter 1962; Chivers 1969; Heltne et al. 1976), parasites (Milton 1996), food shortages (Foster 1982; Milton 1982; Crockett 1996), dietary imbalance, and secondary compounds (Glander 1975, 1978, 1982) have played critical roles in determining densities and population structure of primates (Coelho et al. 1976; Froehlich et al. 1981; Butynski 1990). Such perturbations and 'ecological crunches' must be accounted for in management plans (Johns 1985a).

The seasonality of tropical dry forest can have many influences on monkey populations. Resource limitation may only be operating during the dry season (Terborgh

1986; Dobson and Lyles 1989) when fruit, leaf, and water resources are reduced (Chapman and Chapman 1990; Chapman and Balcomb in press) and ecological roles are most sharply defined (Terborgh 1986). Some studies suggest that semi-evergreen [older] forests produce food at a more constant level throughout the year than deciduous [younger] forests (Chapman and Chapman 1990; Chapman and Balcomb in press). In the dry season, monkeys may spend more time in older forests where there are more large evergreen trees and consequently more leaf food sources, more shade and lower temperatures to avoid dehydration, and more tree holes with drinking water. Furthermore, the availability of insect food may differ between the dry and rainy season in different stages of forest regeneration. In the future, additional variation of monkey densities will be examined by correlating density with food abundance during the rainy and during the dry seasons (in prep). Management practices must account for the lowest abundances of food within each year.

In addition to differences in food availability and monkey densities, the spatial distribution of monkeys may differ between seasons. Species dependent on water for drinking, such as capuchins, may become central-place foragers around water holes in the dry season (Fedigan et al. 1996) and thus become more spatially clumped. There are some observations that spider monkeys may increase their daily ranging distances in the dry season in order to find food (Fedigan pers. comm.). This could increase the chances of being seen in a wider range of regeneration stages; therefore densities may be more evenly distributed among forest ages in the dry season. The sightings of spider monkeys in the 25 year-old forest of the current study were only in the dry season. The influence of the dry and rainy season on group cohesiveness and home range use needs to be examined in the future.

Management Implications

It is clear from the results that regenerating habitat cannot be expected to contain densities of the three monkey species similar to undisturbed forest. Only the undisturbed forest, with an assigned age of 110-130 years old, contained maximum densities of capuchins and spider monkeys. There is, however, potential for the use of regenerating

forest to complement, but not replace, protected undisturbed forest in habitat management plans (Bearder 1991). One example would be a buffer area adjacent to protected parks in which the majority of the forest was maintained at a mid- to mature regeneration state (70-100 years old) through long return intervals for clear-cutting or through low intensity selective harvesting. Such forest might also contain maximum densities of howlers.

It appears that both forest age and food abundance influence the density and group compositions of these monkeys. Managers may be able to increase the density, and the proportion of immatures, of capuchins and howlers in disturbed forests by managing the forest for higher monkey food biomass (Terborgh 1986; Bearder 1991; Johns 1992) such as in the site *Cerco de Piedra*. Residual fruiting trees dramatically increased the abundance of food and primate densities above what would be expected by forest age alone. Many researchers have emphasized the importance of protecting keystone species such as figs that provide the 'base-line' food even during periods of food scarcity such as the dry season (Terborgh 1986; Bearder 1991; Whitmore 1991; Frumhoff 1995). These food trees constitute a small proportion of the trees and wood volume of the forest, and could be left during logging operations with minimal cost (Terborgh 1986). Unfortunately spider monkey densities were not strongly correlated with food biomass and thus management of food biomass may have little impact on spider monkey densities. My results indicate that areas of undisturbed forest must be protected to conserve spider monkey populations.

The most successful management strategies for tropical dry forest will probably incorporate a variety of land-use and protection policies (Johns 1985a). The importance of large areas of undisturbed 'pristine' habitat has been stressed for years and there is little argument (Johns 1985a); however, managers are beginning to obtain the tools to manage primate populations in selectively logged, fragmented, and regenerating habitats. Management of primates in these disturbed areas should not replace the protection of undisturbed forest, but rather work in addition to conservation areas (Johns and Skorupa 1987). Information on selective logging pressures on particular species is beginning to build and become useful in management, mostly in areas other than the neotropics (Wilson and Wilson 1975b; Wilson and Johns 1982; Johns 1985a, 1986, 1988; Skorupa 1986;

Weisenseel et al. 1993). Research has begun on forest fragmentation (Bernstein et al. 1976; Lovejoy et al. 1986; Estrada and Coates-Estrada 1996) but much more is needed on a wider range of species. My results suggest that a portion of the monkey population may be maintained by protecting relatively small (*ca.* 1km^2), but connected, patches of mature forest.

Table 3-1. DISTANCE estimates of effective strip width, μ, for each species-site combination.

		μ		
Site	**Forest Age**	***Cebus***	***Alouatta***	***Ateles***
Quebrada Duende	20	35.7		39.0
Quebrada Guapote	25	18.0		
Cerco de Piedra	40	9.8 [a]	15.4 [b]	
Laguna Escondida	40	28.0 [b]	5.0 [a]	
Cuatro Esquinas	50	27.0	24.4	29.0
Tocon	60	29.0	40.3	27.6
Loma	70	17.9	19.2	38.0
Cuajiniquil	75	25.0	31.2	37.0
Mirador de Naranjo	95	34.1	21.8 [b]	10.0 [a]
Bosque Humedo	110	15.0	17.5	13.8
Quebrada Puercos	130	20.5	19.8	24.5
	Mean	**23.6**	**21.6**	**27.4**

"a" estimate was replaced with "b" estimate (the most abundant species within the site).

Table 3-2. Species of trees used in calculating food abundance for each monkey species. Percent of foraging time for each food item is in brackets.

Capuchin Food Species	Howler Food Species	Spider Food Species
Acacia collinsii -Fruit (3.5) b	*Andira inermis* -Leaves (11.8) e	• *Brosimum alicastrum* -Fruit (2.7) a
• *Bursera simaruba* -Fruit (26.6) b,c	*Astronium graveolens* - Leaves (5.3) d,e	• *Bursera simaruba* -Fruit (2.4) a
• *Chlorophora tinctoria* -Fruit (6.8) c	• *Brosimum alicastrum* -Fruit (5.5), Leaves (14.7) a,d	• *Cecropia peltata* -Fruit ("important") c,t
Coccoloba guanacastensis -Fruit (1) t	• *Bursera simaruba* -Fruit (9.1), Leaves (8.1) a,d,e	*Coccoloba guanacastensis* -Fruit (2.7) a,t
Dipterodendron costaricensus -Fruit (6.0) b,c	*Castilla elastica* -Leaves (2.7) a,d	*Dipterodendron costaricensus* -Fruit (6.3) a
Ficus spp. -Fruit (14.3), Leaves (2.4) a,b,c	*Chlorophora tinctoria* -Leaves (1.4) d	*Ficus* spp. -Fruit (29.2), Leaves (2.4) a
Genipa americana -Fruit (3.6) b,c	*Coccoloba guanacastensis* -Fruit (1) t	*Hymenaea courbaril* -Leaves (2.0) a
Guettarda macrosperma -Fruit (1.1) b	*Cordia panamensis* -Leaves (2.0) d	*Mastichodendron capiri* -Fruit (6.6) a
Hirtella racemosa -Fruit (1.8) b	*Dipterodendron costaricensis* -Fruit (1.8) d	*Muntingia calabura* -Fruit (16.1) a
Luehea candida -Fruit (9.8) b,c	*Ficus* spp. -Fruit (15.5), Leaves (21.7) a,d	• *Sciadodendron excelsum* -Fruit ("important") c
Luehea speciosa -Fruit (4.4) a,b,c	*Gliricidia sepium* -Leaves (1.3) e	*Slonea terniflora* -Fruit (2.2) a
Muntingia calabura -Fruit (17.9) a,b,c	*Hymenaea courbaril* -Leaves (3.4) a,d	• *Spondias mombin* -Fruit ("important") c,t
Quercos oleoides -Fruit (3.5) a,b	*Inga vera* -Leaves (1.1) d	
Randia echinocarpa -Fruit (2.1) b	*Licania arborea* -Leaves (11.5) d,e	
• *Sciadodendron excelsum* -Fruit (2.8) a,b,c	*Manilkara chicle* -Leaves (1.2) d	
• *Simarouba glauca* -Fruit (5.1) b,c	*Mastichodendron capiri* -Fruit (3.1), Leaves (2.2) a,d,e	**Legend**
Slonea terniflora -Fruit (34.1) a,b	*Muntingia calabura* -Fruit (2.9), Leaves (2.9) d,e	a-Chapman 1987 (*Cebus* 171h, *Alouatta* 394h, *Ateles* 335h)
Sterticula apetala - Fruit (1.5) b	*Pithecellobium saman* -Leaves (1.1) d,e	b-Chapman and Fedigan 1990 (*Cebus* 534h)
Swartzia cubensis -Fruit (1.7) b	• *Sciadodendron excelsum* -Fruit (6.3) d	c-Freese 1977 (*Cebus* 180h)
Zuelania guidonia -Fruit (2.1) b	*Simaruba glauca* -Leaves (1.1) d	d-Larose 1996 (*Alouatta* 2040h)
	• *Spondias mombin* -Fruit (1.0) e	e-Glander 1978 (*Alouatta* 2071h)
	Swartzia cubensis -Fruit (3.5) d	t-pers. obs. (assigned 1%)
	Tabebuia rosea -Leaves (1.8) d	• dioecious or sequential hermaphroditic
	Thouinidium decandrum -Leaves (2.6) d	

Table 3-3. Composition of capuchin groups in each study site. Group codes are from Fedigan et al. 1985, and Fedigan unpubl. Age of forest is in brackets.

Site	Group Code	Group Size	Immature: Adult
Quebrada Duende (20)	L	12	0.50
Quebrada Guapote (25)	Na	12	*
Laguna Escondida (40)	J	11	0.33
Cerco de Piedra (40)	N	13	0.57
Cuatro Esquinas (50)	O	16	0.27
Tocon (60)	I	25	0.47
Loma (70)	C	12	0.57
Cuajiniquil (75)	B	22	0.47
Mirador de Naranjo (95)	T	16	0.45
Bosque Humedo (110)	E	15	0.50
Quebrada Puercos (130)	G	13	1.00
Mean		15.2	0.51
Pooled			0.49

* The ages of 4 capuchins in the Quebrada Guapote group were not known so I did not calculate age ratios.

Table 3-4. Composition of howler monkey groups in each study site. Three sites have two howler monkey groups. Group codes are from Fedigan et al. 1985, and Fedigan unpubl. Age of forest is in brackets.

Site	Group Code	Group Size	Male:Female Sex Ratio	Immature: Adult	Immature: Female
Laguna Escondida (40)	8	5	0.33	0.25	0.33
Cerco de Piedra (40)	30	5	0.50	0.67	1.00
Cuatro Esquinas (50)	12	27	0.38	0.23	0.31
	13	20	0.56	0.43	0.67
Tocon (60)	7	13	0.60	0.63	1.00
Loma (70)	3	16	0.33	0.33	0.44
Cuajiniquil (75)	1 + 1a	25	0.64	0.50	0.73
	2	14	0.43	0.40	0.57
Mirador de Naranjo (95)	16a	9	0.50	0.50	0.75
Bosque Humedo (110)	5*	12	0.20	0.33	0.40
	31	8	0.40	0.71	1.00
Quebrada Puercos (130)	6	12	0.29	0.67	0.57
Mean		13.8	0.43	0.47	0.65
Pooled			0.43	0.41	0.59

* subgroup?

Table 3-5. Composition of spider monkey groups in each study site. Age of forest is in brackets.

Site	Minimum Community Size	M:F Sex Ratio	Immature: Adult	Immature: Female	Foraging Party Size		
					Mean	SD	n
Quebrada Duende (20)	11	0.17	0.57	0.67	6.00	3.16	7
Cuatro Esquinas (50)	12	0.20	1.00	1.20	3.83	3.60	6
Tocon (60)	9	1.00	0.50	1.00	5.63	1.41	8
Loma (70)	11	0.33	0.75	1.00	3.83	2.32	6
Cuajiniquil (75)	7	1.00	0.17	0.33	2.64	1.80	11
Mirador de Naranjo (95)	* 2	* 1.00	* 0	* 0	1.33	0.58	3
Bosque Humedo (110)	11	0.60	0.22	0.40	3.69	2.33	36
Quebrada Puercos (130)	25	0.56	0.79	1.22	6.96	4.74	23
Mean		0.55	0.57	0.83	4.24	2.49	8
Pooled Mean		0.51	0.56	0.86	4.59	3.40	100
Pooled Mode					2.00		
Pooled Median					4.00		

* Spiders monkeys observed at *Mirador de Naranjo* were not included in group composition regressions.

Table 3-6. Comparison of monkey densities in upper and lower plateau using different criteria for suitable habitat. Number of monkeys was obtained from the latest census for each monkey group. Areas were calculated from a 80m x 80m grid overlain on a vegetation map of the park (Pacheco and Morera 1986).

Number of Monkeys

	Cebus	Howler
Upper	243	329
Lower	285	291
Total	528	620

Forest Area (km^2)

	Evergreen	Mixed	Deciduous
Upper	6.0	4.5	12.5
Lower	7.4	9.3	27.6
Total	13.4	13.8	40.0

Evergreen Forest Only

	Cebus	Howler
Upper	40.6	54.9
Lower	38.4	39.2
Total	39.3	46.2

Evergreen and Mixed Forest

	Cebus	Howler
Upper	23.2	31.3
Lower	17.1	17.4
Total	19.4	22.8

Evergreen, Mixed, and Deciduous Forest

	Cebus	Howler
Upper	11.3	15.2
Lower	6.4	6.6
Total	8.0	9.4

Figure 3-1. Connectivity of forest within Santa Rosa National Park. Dark shading indicates areas with large trees, semi-continuous canopy, and where all three monkey species can travel through. Light shading indicates areas of small, short trees where arboreal travel may be impeded. Areas without shading have very few trees and travel would be primarily terrestrial. Transects and study sites are numbered 1-14.

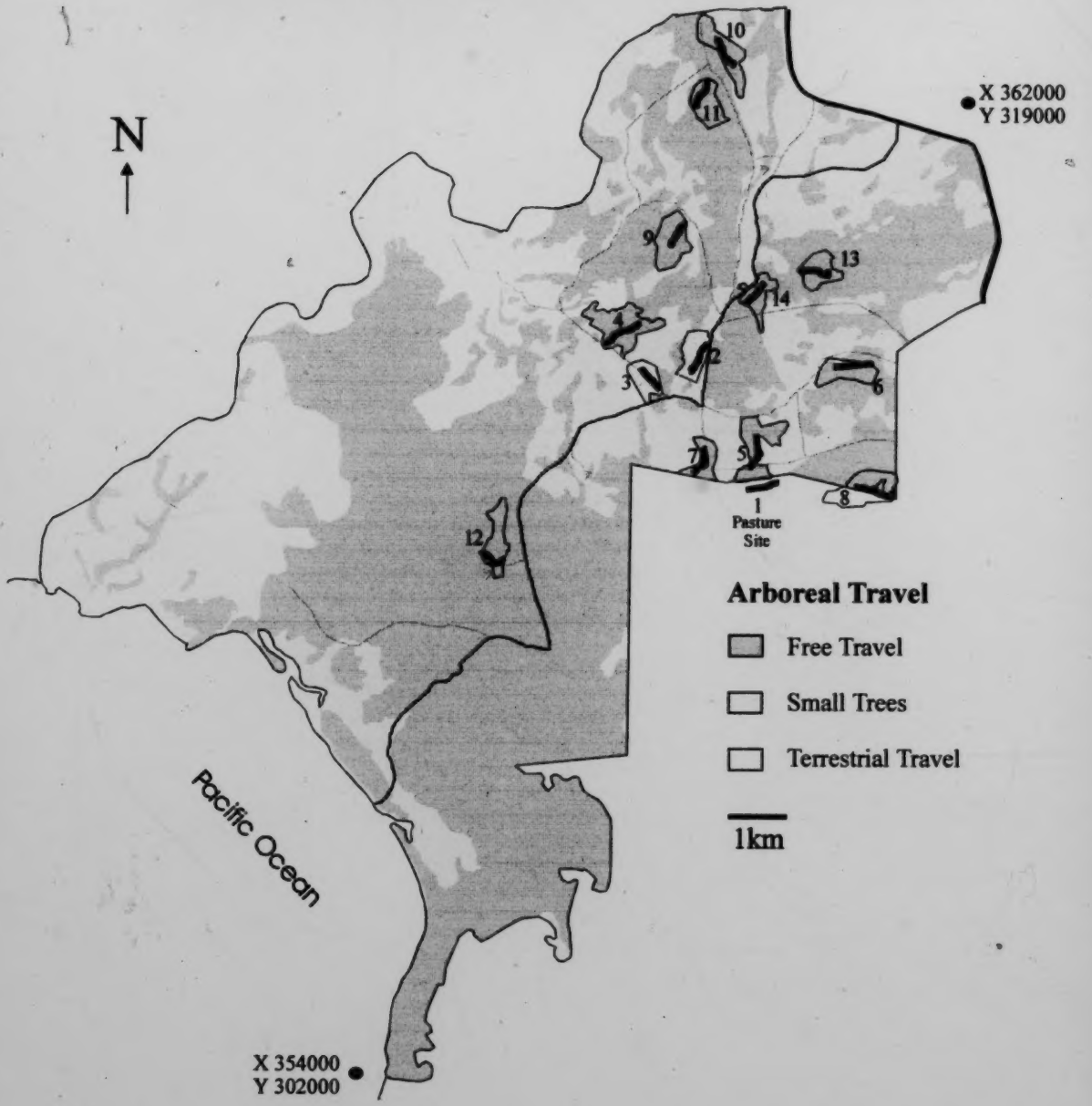


Figure 3-2. Location of all known capuchin groups (*Cebus capucinus*) within Santa Rosa National Park. Groups are indicated with letters. Study sites are bordered with solid line as in Figure 3-1.

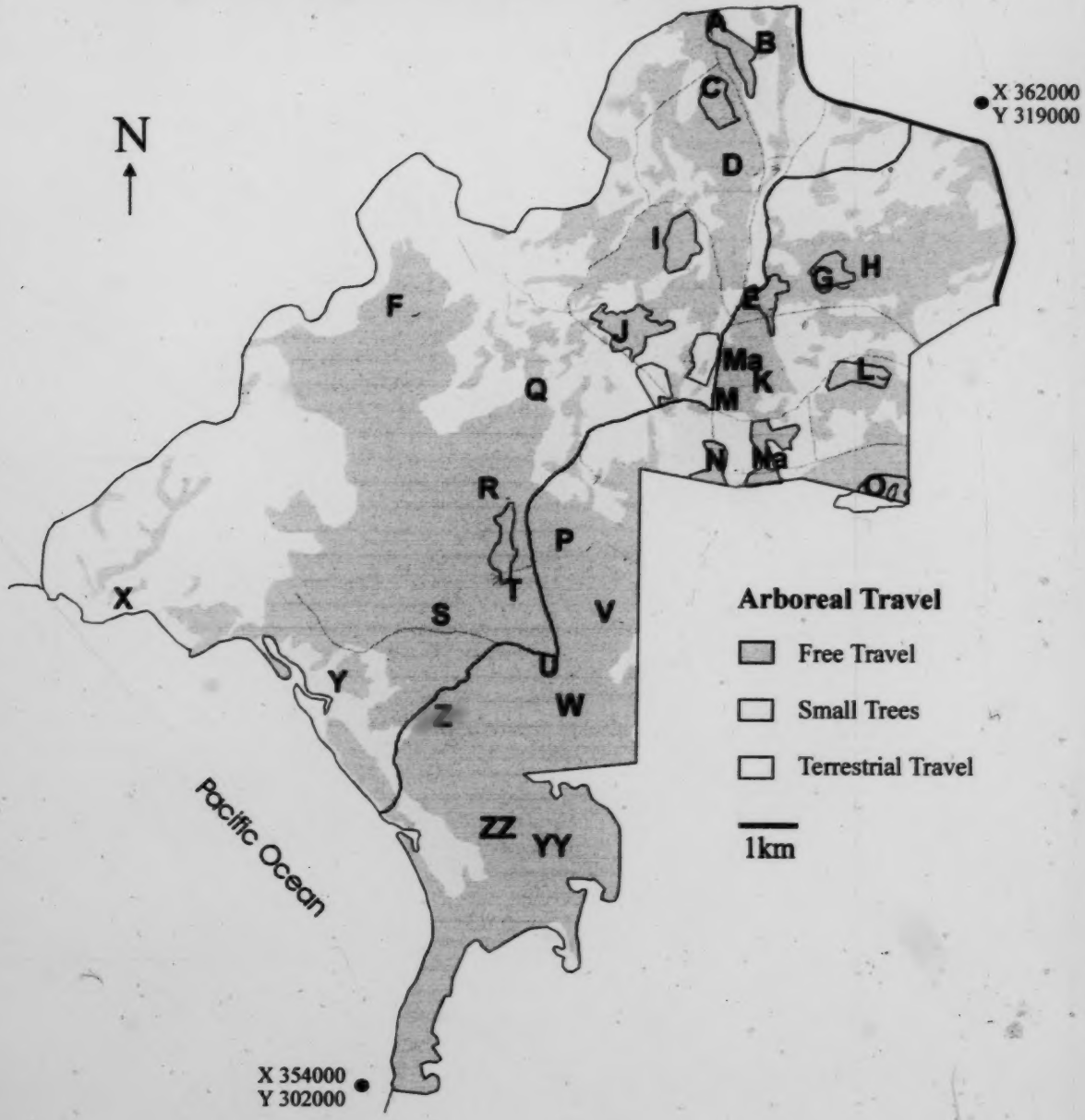


Figure 3-3. Location of all known howler groups (*Alouatta palliata*) within Santa Rosa National Park. Howler groups are indicated with numbers. Study sites are bordered with solid line as in Figure 3-1.

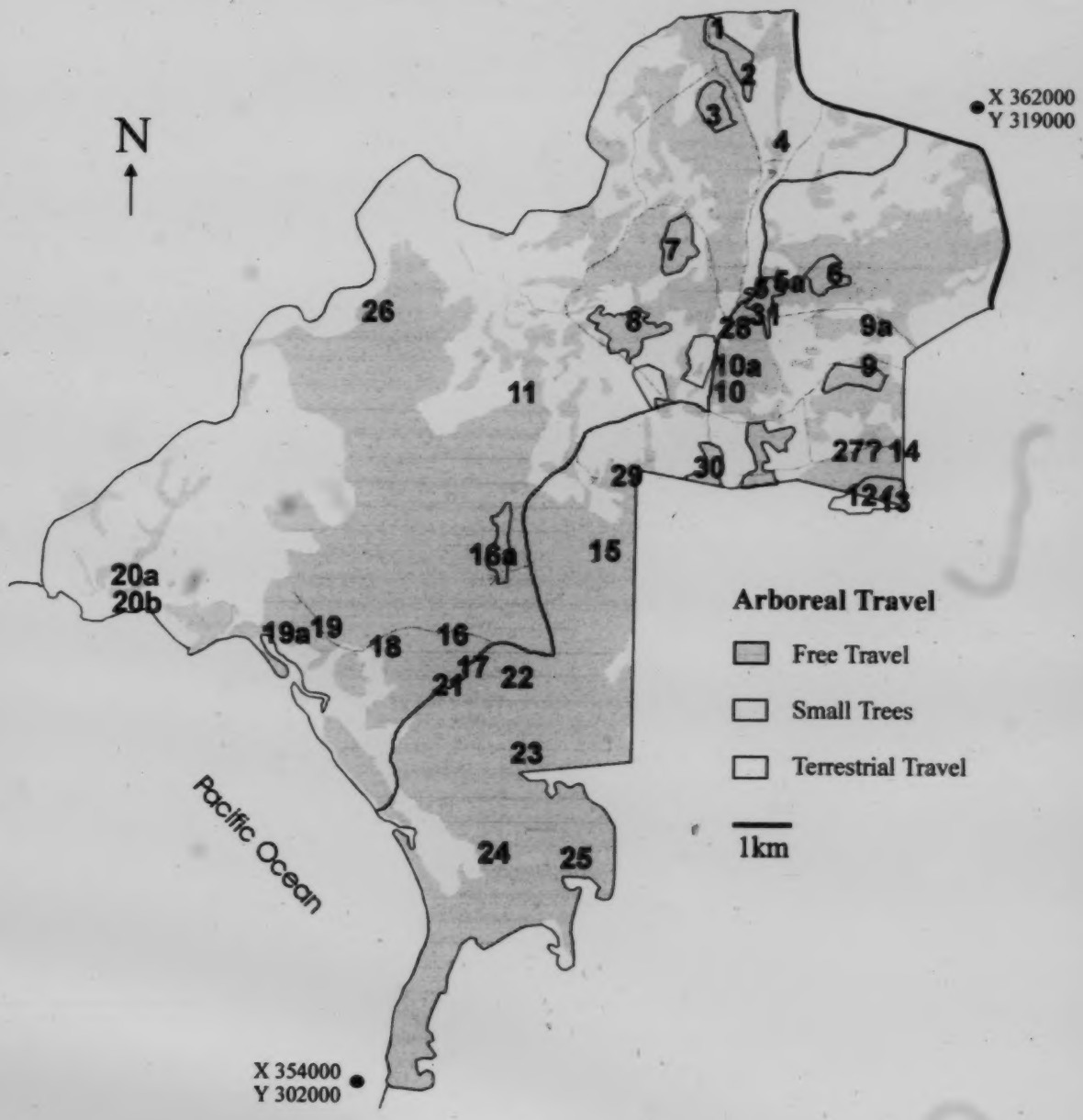


Figure 3-4. The uniform + cosine detection function used by DISTANCE for howling monkeys in *Quebrada Puercos* (Table 2-1). Number of monkeys is also plotted (histogram) with the number observed above each column.

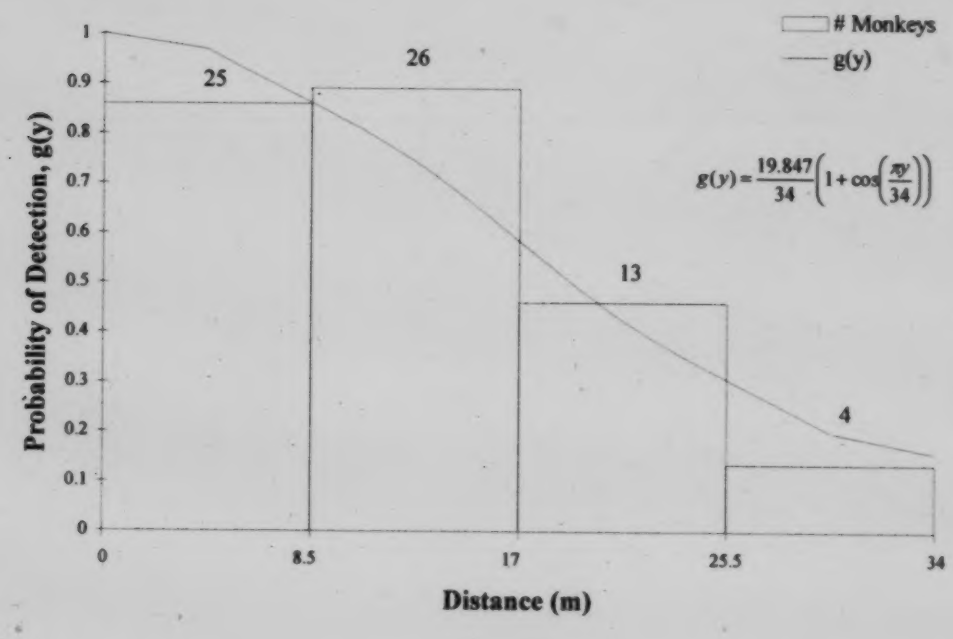


Figure 3-5. Percent precision and density as sample size (number of transects walked) increased for capuchins (◆), howler monkeys (□), and spider monkeys (▲) in *Quebrada Puercos*. Similar trends were found for the rest of the species / site combinations.

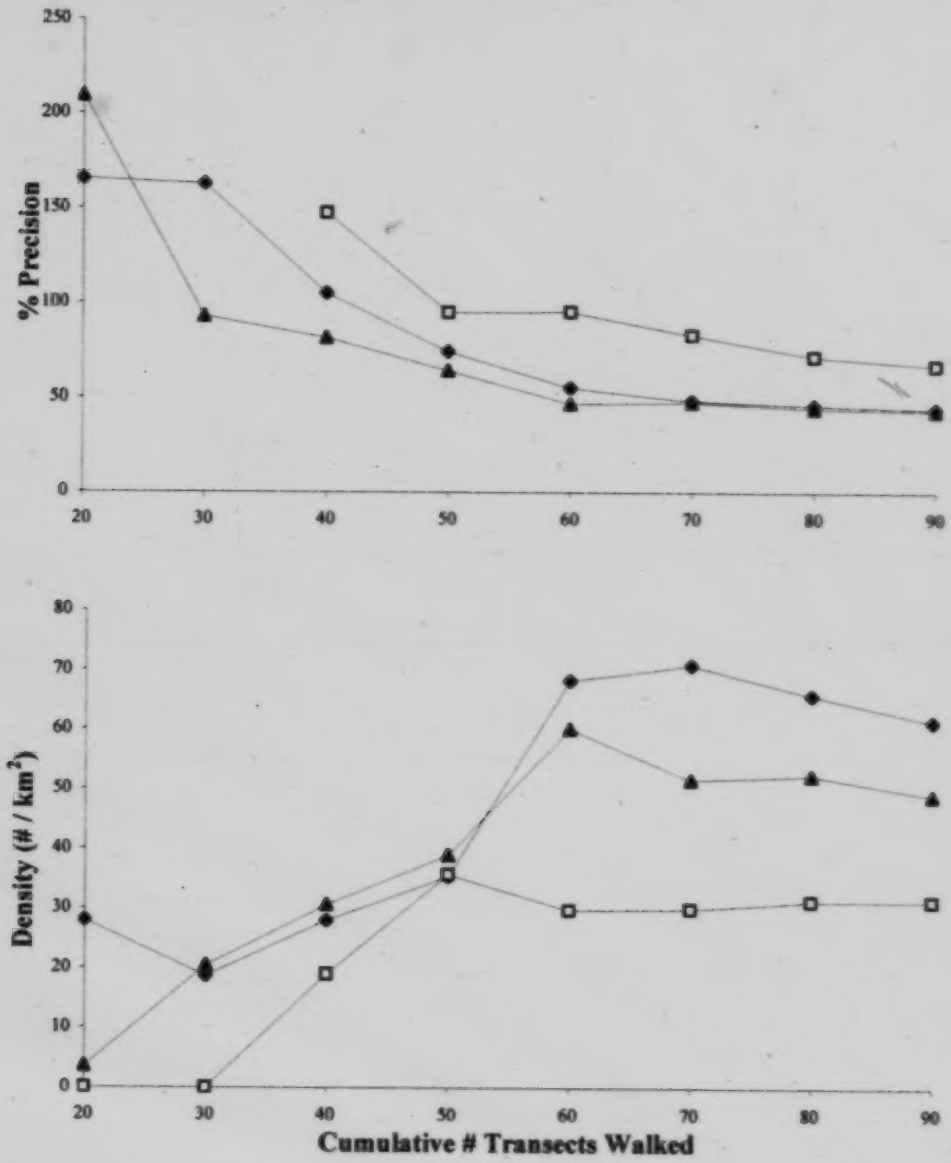


Figure 3-6. Density (+/- Standard Error, SE) of white-faced capuchins (*Cebus capucinus*) along a regeneration gradient. Density in *Cerco de Piedra* (a) may be inflated by a large number of residual fruiting trees.

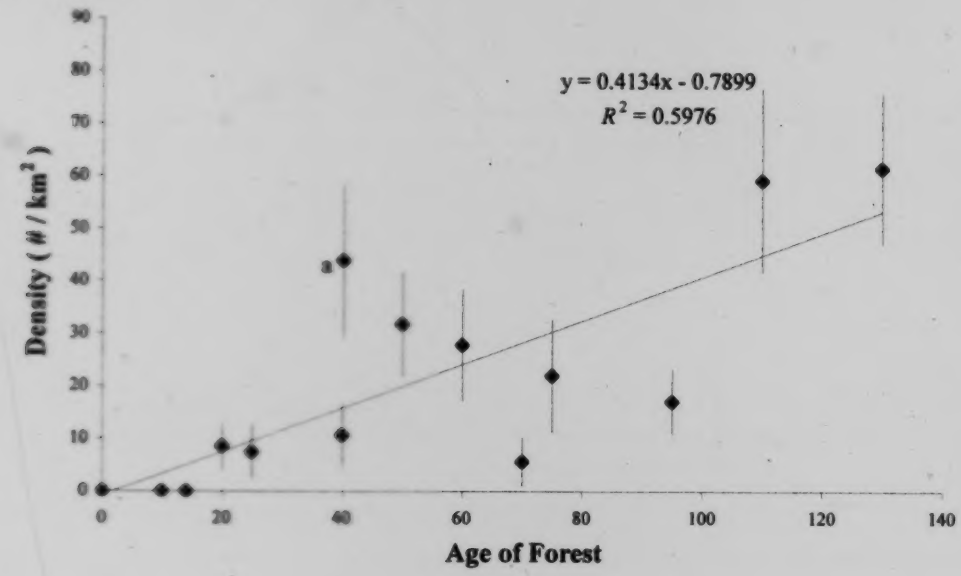


Figure 3-7. Density (+/- SE) of howler monkeys (*Alouatta palliata*) along a regeneration gradient. Density in *Cerco de Piedra* (a) may be inflated by a large number of residual fruiting trees. The majority (90%) of sightings in *Cuatro Esquinas* (b) were within two areas of older forest (70-90 yrs old).

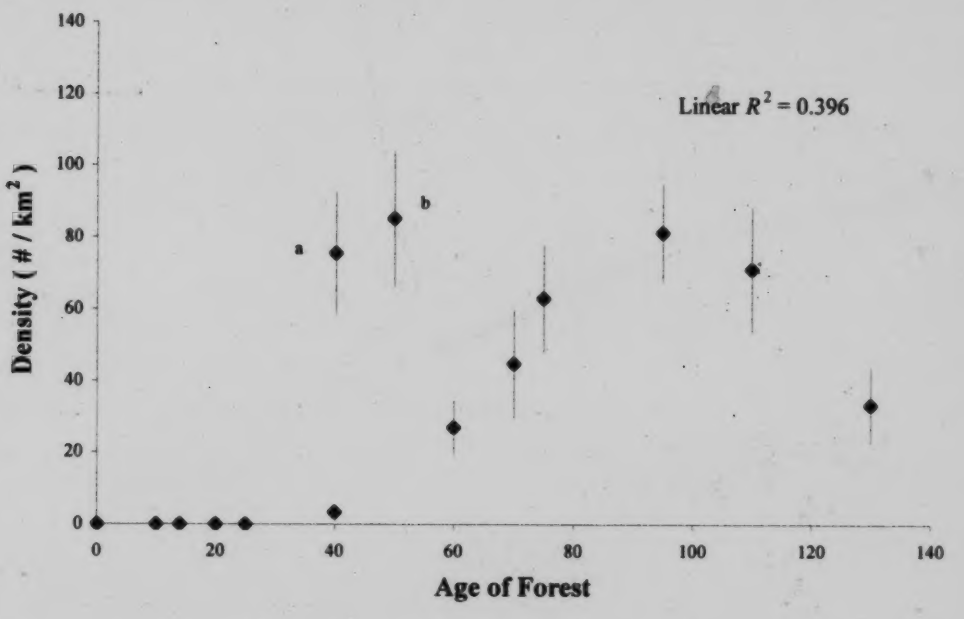


Figure 3-8. Density (+/- SE) of spider monkeys (*Ateles geoffroyi*) along a regeneration gradient.

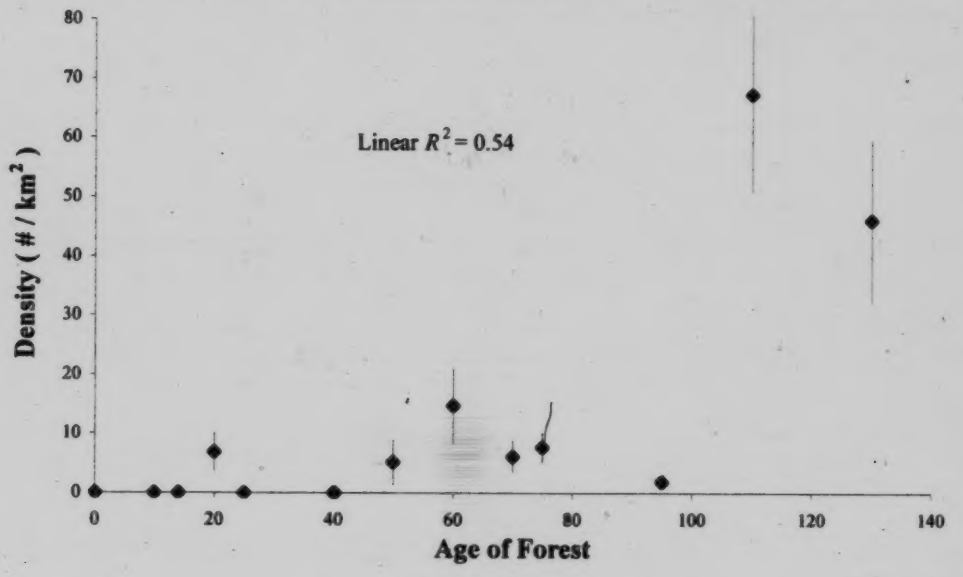


Figure 3-9. A plot of capuchin density (+/- SE) vs. the abundance of capuchin food based on fruit items that constitute at least 2% of diet. The log(density) vs. log (fruit biomass) regression improves heteroscedasticity with R^2=0.822. The food biomass was highest in *Cerco de Piedra* (a) due to residual fruiting trees.

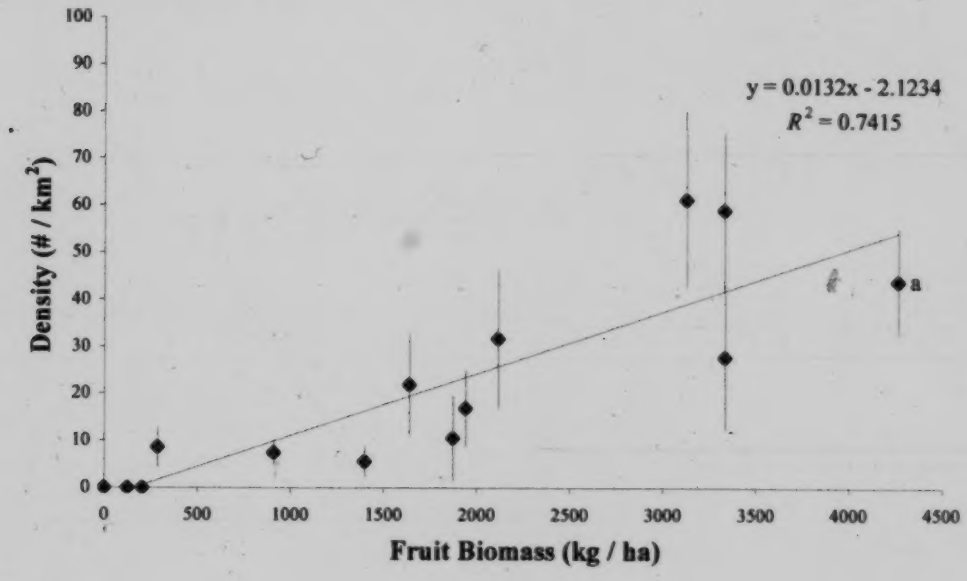


Figure 3-10. A plot of howler densities (+/- SE) vs. the abundance of howler food (items >1.9% of diet). The food biomass and howler density in *Cerco de Piedra* (a) was higher than other sites of similar forest age due to residual fruiting trees. The majority (90%) of sightings in *Cuatro Esquinas* (b) were within two areas of older forest (70-90 yrs old) which probably had higher food biomass/ha.

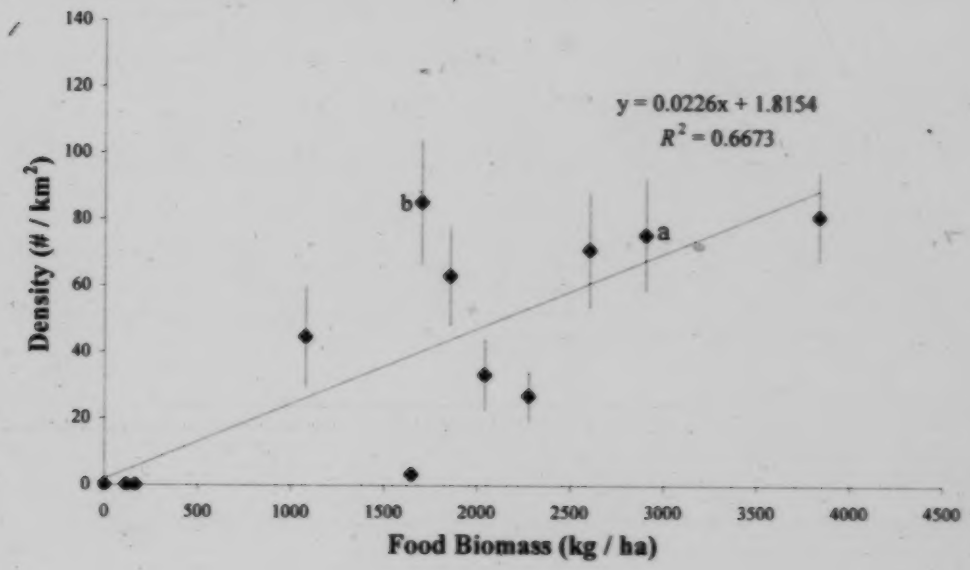


Figure 3-11. A plot of spider monkey densities (+/- SE) vs. the abundance of spider monkey food, based on items that constitute at least 2% of diet. The food biomass in *Cerco de Piedra* (a) was higher than other sites of similar forest age due to residual fruiting trees.

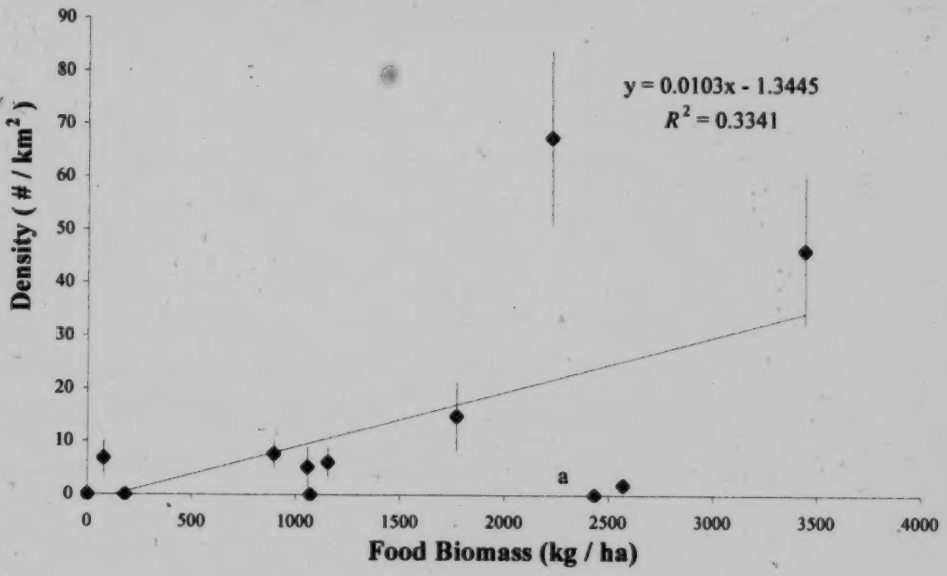


Figure 3-12. Fruit biomass of capuchin diet (items >1.9% of diet) along a regeneration gradient. The food biomass in *Cerco de Piedra* (a) was higher than other sites of similar forest age due to residual fruiting trees.

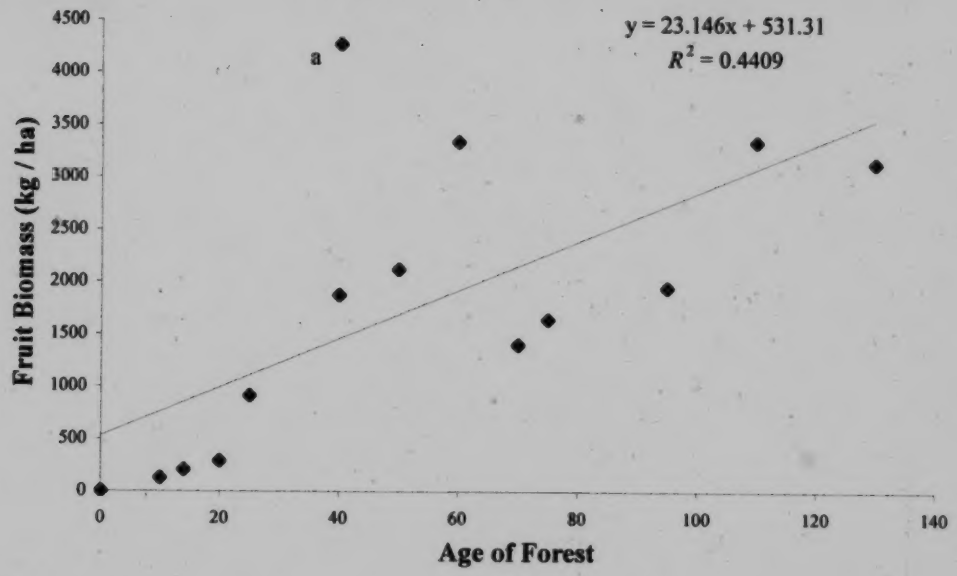


Figure 3-13. Biomass of howler food (items>1.9% of diet) along a regeneration gradient. A log (food biomass) vs. log (forest age) regression improved heteroscedasticity with R^2=0.734. The food biomass in *Cerco de Piedra* (a) was higher than other sites of similar forest age due to residual fruiting trees.

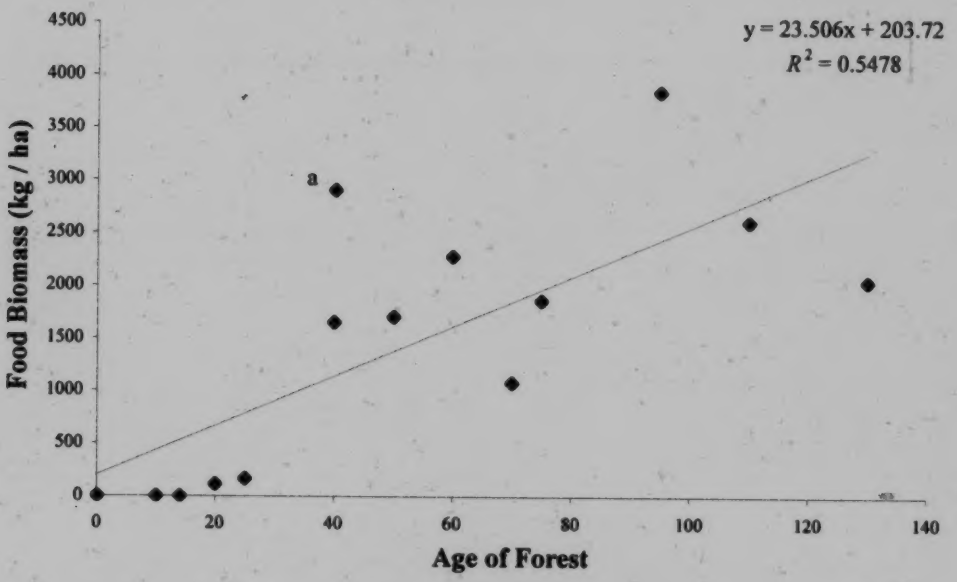


Figure 3-14. Biomass of spider monkey food (items >1.9% of diet) along a regeneration gradient. The food biomass in *Cerco de Piedra* (a) was higher than other sites of similar forest age due to residual fruiting trees.

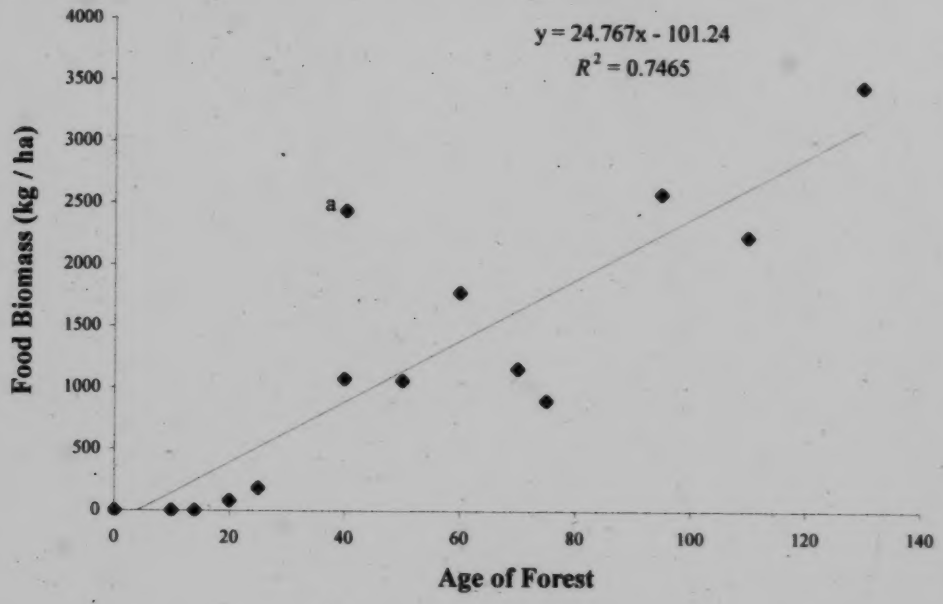
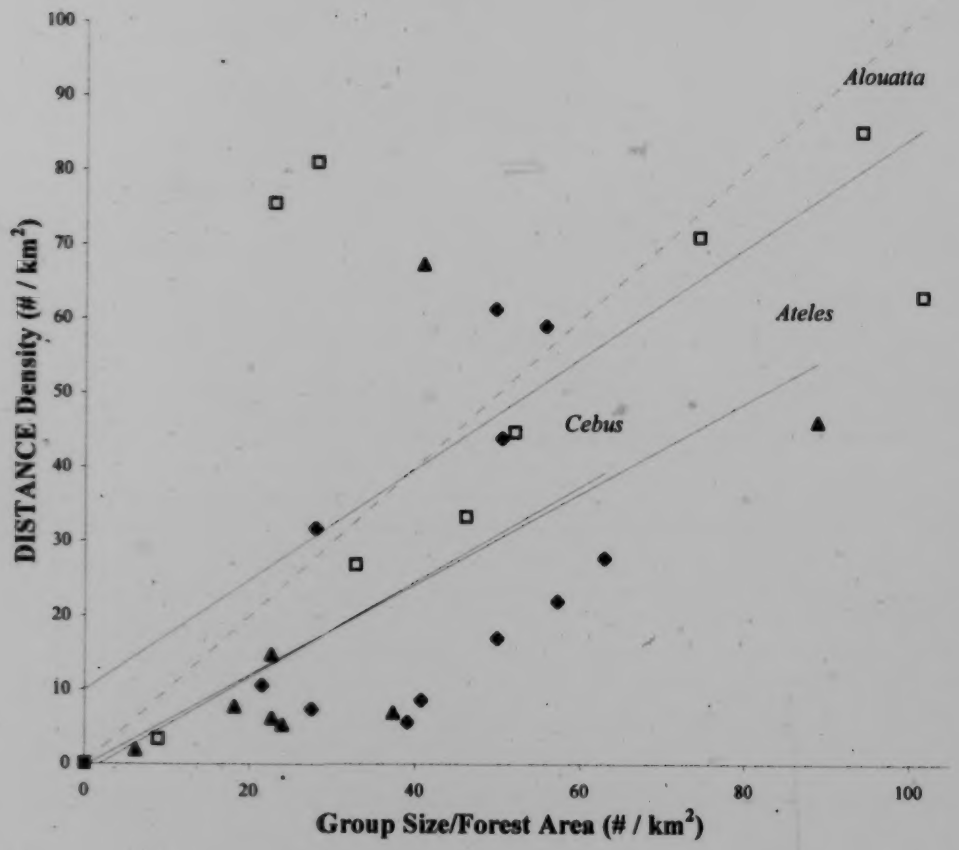


Figure 3-15. Comparison of density estimates calculated by DISTANCE and group size/forest area method. Dotted line represents a perfect 1:1 correlation. DISTANCE estimates for capuchins (◆, R^2 = 0.46), howlers (□, R^2 = 0.60) and spider monkeys (▲, R^2 = 0.57) were significantly correlated with the group size/forest area estimates. Howler monkey group sizes were summed in forests with two howler groups. Monkeys in sites above the 1:1 ratio may have used only a portion of the patch. Monkeys in sites below the 1:1 ratio may have used forest in addition to the patch.



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IV. General Discussion

The preceding chapters contribute to the understanding of tropical dry forest regeneration and its influence on three species of monkeys. In the introductory chapter, the conservation status of tropical dry forest is defined with emphasis on the need for more research on the ability of the ecosystem to regenerate. The original area of tropical dry forest has been seriously reduced and is now the most endangered lowland tropical forest type (Janzen 1988). Protection of the remaining intact patches would be insufficient to save the ecosystem; therefore the only other option available to conservationists is the regeneration of disturbed areas. The effects of deforestation and fragmentation on the wildlife of tropical dry forest are yet unknown and even less is known about the ability of wildlife to use regenerating habitat. I propose the use of neotropical monkeys to indicate the amount of regeneration required to attract and sustain natural populations of wildlife. Only by understanding tropical dry forest regeneration can conservationists develop sustainable management plans.

In chapter 2, the structure and tree species composition of tropical dry forest is examined along a regeneration gradient. Community level analyses of the tree species indicated that species turnover was highest during the first 40 years of succession and species richness peaked between 50 and 70 years of regeneration. Likewise, most of the forest structure was regained in 40 to 50 years. The community analysis also associated the major tree species with different regeneration stages. This research provides some of the tools to develop management strategies based on specific goals for regenerating forest, such as forest structure, species diversity, and/or species composition.

In chapter 3, I examine the influence of this forest regeneration gradient on the densities and group compositions of three sympatric monkey species: white faced capuchins (*Cebus capucinus*), mantled howling monkeys (*Alouatta palliata*), and spider monkeys (*Ateles geoffroyi*). This study is the first to document neotropical primate densities within the full range of forest regeneration. Systematic and objective transect

methods assessed the ability of each species to use a wide range of regeneration stages. Detailed tree data from Chapter 2 provided explanations for the proximate influences of regeneration on the monkey densities and group compositions. The results indicate that natural populations of all three species will only occur in protected areas of undisturbed forest. On the other hand, the densities and group compositions of capuchins and howlers were most strongly related to food abundance which can be managed by leaving fruit trees, such as figs, in abandoned pastures. In future management plans, monkey populations in regenerating forest may complement the populations in protected areas of mature forest.

To study the reclamation of habitat for vulnerable populations, species-specific ecological and behavioral factors must be taken into account (Fedigan et al. in press). The result of this study support predictions that species with large body size, low reproductive rate, and frugivorous diet have less tolerance for the earlier regeneration stages.

Future Research

To better estimate the age of tropical dry forests researchers need species-specific growth rates for trees. This research is in progress (B. Enquist pers. comm.) and will greatly aid the study of tropical dry forest regeneration. Only then can the demography and dynamics of dry forest regeneration be studied in greater detail.

The densities of monkeys were correlated with crude estimates of food biomass; however much more detailed food biomass estimates could be obtained with species-specific allometric relationships between tree size and fruit, leaf, and flower biomass. Energetic analyses of diet items will also allow a better understanding of food quality rather than relying on total biomass.

The ability of the three monkey species to utilize regenerating habitat may depend solely on the quality of habitat in the dry season (Freese 1976). The next stage in dry forest regeneration research is to evaluate the influence of the dry/rainy season on the quality of habitat at various stages of regeneration. Several researchers have suggested that resource competition is higher during the dry season, which would be the time when ecological roles are most clearly defined (Terborgh 1986).

Further research is needed on the influence of forest regeneration and monkey density on behavior. Butynski (1990) recognized that a disproportionate number of primate studies are done in areas of unusually high densities; therefore the perceptions of species' characteristics are influenced by high densities and its correlates. In a few studies, primate density has been shown to influence infanticide, territoriality, tenure lengths of males in groups, male-male competition for females, male reproductive success, home range area, group fissioning, diet selectivity, and aggression (Altmann and Altmann 1979; Butynski 1990).

Results from this study may be used in developing conservation and management plans not only for primates but also for tropical dry forest in general. The use of a regeneration gradient has proved useful in examining the ability of wildlife to use regenerating habitat; however, much more conclusive information will come from long-term studies on multiple sites, such as the work started in Santa Rosa National Park.

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Appendix 1. Known species of trees found in the 13 study sites.

Species Name	Family	Structure	Dispersal	Leafing	Leaf Structure
Acacia collinsi	Mimosaceae	U	A	-	C
Acacia farnesiana	Mimosaceae	U	A	-	C
Acrominae vinifera	Palmae	S	A	-	C
Agonandra macrocarpa	Opiliaceae	S	A	-	-
Albizzia adinocephala	Mimosaceae	C	W	D	C
Alibertia edulis	Rubiaceae	U	A	EG	S
Allophylllus psilospermus	Sapindaceae	S	A	-	C
Andira inermis	Fabaceae	C	A	EG	C
Annona purpurea	Annonaceae	S	A	D	S
Annona reticulata	Annonaceae	S	A	D	S
Apeiba tibourbou	Tiliaceae	S	A	D	S
Ardisia revoluta	Myrsinaceae	U	A	EG	S
Astronium graveolens	Anacardiaceae	C	W	D	C
Ateleia herbert-smithii	Fabaceae	C	W	D	C
Bauhinia ungulata	Caesalpinaceae	U	W	D	S
Bombacopsis quinatum	Bombacaceae	C	W	D	C
Brosimum alicastrum	Moraceae	C	A	EG	S
Bunchozia sp.	Malpighiaceae	U	A	-	S
Bursera simaruba	Burseraceae	C	A	D	C
Bursera tomentosa	Burseraceae	C	A	D	C
Byrsonima crassifolia	Malpighiaceae	S	A	EG	S
Calycophyllum candidissimun	Rubiaceae	C	W	D	S
Capparis indica	Capparidaceae	S	A	-	S
Casearia arguta	Flacourtiaceae	S	A	D	S
Casearia corymbosa	Flacourtiaceae	U	A	D	S
Casearia praecox	Flacourtiaceae	S	A	-	S
Casearia sylvestris	Flacourtiaceae	S	A	-	S
Cassia grandis	Caesalpinaceae	C	A	D	C
Castilla elastica	Moraceae	C	A	D	S
Cecropia peltata	Moraceae	S	A	D	C
Cedrela odorata	Meliaceae	C	W	D	C
Ceiba pentandra	Bombacaceae	C	W	D	C
Chlorophora tinctoria	Moraceae	C	A	D	S
Chomelia spinosa	Rubiaceae	S	A	-	S
Coccoloba guanacastensis	Polygonaceae	C	A	EG	S
Cochlospermum vitifolium	Cochlospermaceae	S	W	D	C
Cordia alliodora	Boraginaceae	C	W	D	S
Cordia panamensis	Boraginaceae	S	A	D	S
Crescentia alata	Bignoniaceae	S	A	D	C
Crescentia cujete	Bignoniaceae	U	A	-	S
Cupania guatemalensis	Sapindaceae	U	A	-	C
Curatella americana	Dilleniaceae	U	A	EG	S
Dalbergia retusa	Fabaceae	C	W	D	C
Diospyros nicaraguensis	Ebenaceae	S	A	-	S
Diphysa robinioides	Fabaceae	S	W	-	-
Dipterodendron costaricensis	Sapindaceae	S	-	-	C
Enterolobium cyclocarpum	Mimosaceae	C	A	D	C
Eugenia salamensis	Myrtaceae	S	A	-	S
Exostema mexicanum	Rubiaceae	S	-	-	S
Faramea occidentalis	Rubiaceae		A	D	S
Ficus spp.	Moraceae	C	A	EG	S
Genipa americana	Rubiaceae	S	A	D	S

Species Name	Family	Structure	Dispersal	Leafing	Leaf Structure
Gliricidia sepium	Fabaceae	S	-	D	C
Guazuma ulmifolia	Sterculiaceae	S	A	D	S
Guettarda mecrosperma	Rubiaceae	S	A	-	S
Hemiangium excelsium	Hippocrateaceae	S	W	-	S
Hirtella racemosa	Chrysobalanaceae	U	A	-	S
Hura crepitans	Euphorbiaceae	C	W	D	S
Hymenaea courbaril	Caesalpinaceae	C	A	EG	C
Inga vera	Mimosaceae	S	A	EG	C
Ixora floribunda	Rubiaceae	S	A	-	S
Jacquinia pungens	Theophrastaceae	U	A	D	S
Karwinskia calderoni	Rhamnaceae	C	A	D	S
Licania arborea	Chrysobalanaceae	C	A	EG	S
Lonchocarpus acuminatus	Fabaceae	C	W	D	C
Lonchocarpus costaricensis	Fabaceae	C	W	D	C
Lonchocarpus minimiflorus	Fabaceae	S	W	D	C
Luehea candida	Tiliaceae	S	W	D	S
Luehea speciosa	Tiliaceae	S	W	D	S
Machaerium kegelii	Fabaceae	S	W	-	C
Malpighia glabra	Malpighiaceae	U	A	-	S
Manilkara chicle	Sapotaceae	C	A	EG	S
Mastichodendron capiri	Sapotaceae	C	A	EG	S
Maytenis jamaicensis	Celastraceae	S	A	-	S
Mouriri myrtilloides	Melastomaceae	U	A	EG	S
Muntingia calabura	Elaeocarpaceae	S	A	-	S
Ocotea veraguensis	Lauraceae	S	A	EG	S
Ouratea lucens	Ochnaceae	U	A	-	S
Picramnia quaternaria	Simaroubaceae	S	A	-	C
Pisonia macranthocarpa	Nyctaginaceae	U	A	-	S
Pithecellobium platylobum	Mimosaceae	U	A	-	C
Pithecellobium saman	Mimosaceae	C	A	D	C
Plumeria rubra	Apocynaceae	C	-	D	S
Pouteria reticulata	Sapotaceae	C	A	EG	S
Psidium guajava	Myrtaceae	U	A	-	S
Quercus oleoides	Fagaceae	C	-	EG	S
Randia echinocarpa	Rubiaceae	S	A	-	S
Rehdera trinvervis	Verbenaceae	S	W	-	S
Rourea glabra	Connaraceae	U	A	EG	C
Sapium thelocarpum	Euphorbiaceae	S	A	-	S
Sapranthus palanga	Annonaceae	S	A	D	S
Schoepfia schreberi	Olacaceae	U	-	-	S
Sciadodendron excelsum	Araliaceae	S	A	-	C
Simaruba glauca	Simaroubaceae	C	A	D	C
Sloanea terniflora	Elaeocarpaceae	C	A	EG	S
Spondias mombin	Anacardiaceae	C	A	D	C
Spondias purpurea	Anacardiaceae	S	A	D	C
Stemmadenia obovata	Apocynaceae	S	A	D	S
Sterculia apetala	Sterculiaceae	C	A	D	C
Swartzia cubensis	Caesalpinaceae	S	A	EG	C
Swietenia macrophylla	Meliaceae	C	W	D	C
Tabebuia ochraceae	Bignoniaceae	C	W	D	C
Tabebuia rosea	Bignoniaceae	C	W	D	C
Thouinidium decandrum	Sapindaceae	S	W	EG	C
Trichilia colimana	Meliaceae	S	A	-	C
Trichilia hirta	Meliaceae	S	A	D	C

Species Name	Family	Structure	Dispersal	Leafing	Leaf Structure
Trichilia tomentosa	Meliaceae	S	A	-	C
Trichilia trifolia	Meliaceae	U	A	-	C
Vernonia trifloscculosa	Asteraceae	U	-	-	S
Xanthoxylum setulosum	Rutaceae	S	-	D	C
Ximenia americana	Olacaceae	U	A	-	S
Xylosma flexuosum	Flacourtiaceae	U	-	-	S
Zuelania guidonia	Flacourtiaceae	C	A	D	S

Abbreviations: Structure = Canopy (C) / Subcanopy (S) / Understory (U); Dispersal = Animal (A) / Wind (W); Leafing = Deciduous (D) / Evergreen (EG); Leaf Structure = Compound (C) / Simple (S); "-" refers to unknown or not applicable characteristic.
Nomenclature used from Janzen and Liesner (1980).

Appendix 2. Composition of monkey groups or communities in the study areas of Santa Rosa National Park. Group codes are from Fedigan et al. 1985, and Fedigan unpubl.

Species	Site	Group Code	Adult Males	Adult Females	Adult	Immature	Infant	Total
Cebus capuchinus	Quebrada Duende (20)	L	3	1	8	3	1	12
	Quebrada Guapote (25)	Na	2	1	7	1	0	12
	Laguna Escondida (40)	J	5	2	9	2	1	12
	Cerco de Piedra (40)	N	5	2	7	2	2	11
	Cuatro Esquinas (50)	O	5	2	11	2	1	14
	Tocon (60)	I	12	5	17	5	3	25
	Loma (70)	C	3	2	7	3	1	12
	Cuajiniquil (75)	B	11	4	15	4	3	22
	Mirador de Naranjo (95)	T	8	3	11	4	1	16
	Bosque Humedo (110)	E	5	2	10	4	1	15
	Quebrada Puercos (130)	G	4	2	7	5	2	14
Alouatta palliata	Laguna Escondida (40)	8	1	3	4	1	0	5
	Cerco de Piedra (40)	30	1	2	3	1	1	5
	Cuatro Esquinas (50)	12	6	16	22	3	2	27
		13	5	9	14	5	1	20
	Tocon (60)	7	3	5	8	3	2	13
	Loma (70)	3	3	9	12	3	1	16
	Cuajiniquil (75)	1 + 1a	7	9	16	5	3	25

Species	Site	Group Code	Adult Males	Adult Females	Adult	Immature	Infant	Total
		2	3	7	10	3	1	14
	Mirador de Naranjo (95)	16a	2	4	6	2	1	9
	Bosque Humedo (110)	5*	1	5	6	1	1	8
		31	2	5	7	3	2	12
	Quebrada Puercos (130)	6	2	7	9	1	1	13
Ateles geoffroyi	Quebrada Duende (20)		1	6	7	2	2	11
	Cuatro Esquinas (50)		1	5	6	3	3	12
	Tocon (60)		3	3	6	2	1	9
	Loma (70)		1	3	4	1	2	7
	Cuajiniquil (75)		3	3	6	0	1	7
	Mirador de Naranjo (95)		1	1	2	0	0	2
	Bosque Humedo (110)		3	5	9	1	1	11
	Quebrada Puercos (130)		5	9	14	5	6	25

Immature were distinguished from infants by their ability to travel independently from adults.

Male and female capuchins were probably not distinguished accurately.

Appendix 3. Density Methodology and the Theory of Transect Sampling: Answers to Common Questions and Concerns.

The following provides answers to some of the questions and concerns raised about density concepts and the use and interpretation of transect methods to estimate densities. I propose that density must be interpreted in light of its dependence on the following 'Factors':

1. spatial scale of the study area
2. the time frame of the study
3. the number of individual monkeys that can ever be found within the study area
4. and the percent of time each individual spends within the study area (Wilson and Wilson 1975).

Within the current study Factors 1 and 2 are held constant.

TRANSECT DENSITY ESTIMATES

1. Concern with the repeated sampling of transects.

Repeated sampling of transects is very common in the primate literature (Wilson and Wilson 1975; Cant 1978; Freese et al. 1982; Defler and Pintor 1985; Chapman et al. 1988; Weisenseel et al. 1993; Fimbel 1994; Peres in press) and has been suggested as the only way to obtain accurate estimates (Wilson and Wilson 1975; Chapman et al. 1988). The only statistical assumption is that repeated samples are "done at time intervals large enough so that the stochastic errors of successive samples are not highly dependent" (Buckland et al. 1996). I resampled transects on 1.5 to 2 day intervals which should have given monkey groups adequate time to redistribute themselves within the forest patch. The distance traveled each day for each species ranges from 1000-3000m/day for capuchins (Robinson and Janson 1987), 250-960m/day for howlers (Larose 1996), and 500-5000m/day for spider monkeys (*Ateles* spp., Robinson and Janson 1987).

2. *A high proportion of zeros in the data for the number of monkeys observed each time a transect was walked.*

This is reflected in the large variance in density estimates due to variable encounter rates (57.6-100% of variance) rather than the estimation of μ (0-42.4%). In other words, the average number of monkeys that were seen each time the transect was walked introduced the most variation to the density estimate. In the future, longer transects (looped if necessary) within a forest patch would increase the encounter rate by sampling more of the forest patch (and monkey group's home range, Wilson and Wilson 1975) and decrease the variance in the density estimates.

3. *Dependence of density estimates on the placement of transects with respect to the distribution of monkeys and the distribution of their food resources.*

Assumption #1 (page 44) of transect theory requires that transects are placed randomly with respect to the distribution of the monkeys (Buckland et al. 1996). The ideal study would have replicates of several forest ages and therefore one could evaluate the variance introduced by transect methods and monkey distribution within and between forest patches of the same age. On the other hand, there is considerable variance associated with each density estimate that probably reflects these random effects.

4. *Effect of diurnal activity and forest structure on density estimates that are based on visibility.*

It has been suggested that transects should only be sampled during peak times of primate activity, early morning and dusk (Wilson and Wilson 1975; National Research Council 1981; Cant 1982). These early studies used fixed width methods that assumed maximum visibility and were not sensitive to changes in μ during the day or with changes in weather. μ will change with the proportion of data from non-active/active times of the day.

The detectability (μ) of monkeys showed no consistent trend with forest regeneration (Table 3-1). Detectability is related to the openness of the forest (Bibby and Buckland 1987) which is probably not linearly related to regeneration because of decreasing tree density (Fig. 2-14) and increasing evergreenness (Fig. 2-6). In all habitats differences in

primate detectability is controlled for by the detection function (Skorupa 1987, see Buckland et al. 1996). I recommend that primate studies in the future use an objective and rigorous method to determine strip width, such as with DISTANCE, rather than visual inspection of distance distributions (e.g. Cant 1978). DISTANCE recognizes error in the strip width estimate and incorporates that error into the variance of the density estimate.

5. *Interpretation of group densities rather than individual monkey densities because individuals are not located independently.*

Assumption #5 of transect theory (page 44) requires that cohesive groups should be counted as clusters rather multiple individuals (Buckland et al. 1996). However, the estimation of group density relies strongly on determining the distance from the center of the group to the transect. In the current study, especially with capuchins and spider monkeys, individuals were highly dispersed within a group. Chapman (1990) found that capuchin groups could be dispersed over a radius of 250m (see also Freese 1976). In order to analyze densities as group units rather than individuals, group size must be accurately known for groups that are directly on the transect (Buckland et al. 1996); however, I recorded many cases in which the center of the group appeared to be directly on the transect but not all individuals (peripherals) were within visual distance. Failure of assumption #5 has little to no effect on density but underestimates variance (Buckland et al. 1996); in other words it does not incorporate the variance in the calculation of average cluster size. If assumption #1 is met and a robust estimator of variance is used, assumption #5 can be ignored (Buckland et al. 1996). For the above reasons the densities were analyzed as individual density rather than group density (see also Chapman et al. 1988; Peres in press).

DENSITY METHODOLOGY

6. *The exact density of monkeys can be calculated as group size divided by forest area. Transect methods provide estimates of habitat 'use'.*

Habitat 'use' and density are not mutually exclusive and are part of the same concept. I suspect that when people refer to 'use' they are suggesting the situation where Factors 1-3

are held constant and Factor 4 is variable; however, I have not found a definition for 'use' in the literature.

The *delimited area* density estimate assumes that groups use entire forest patches uniformly and that groups spend all of their time within the patches. This probably explains why delimited area density estimates were often higher than DISTANCE densities.

7. *The large differences between the group size/forest area densities and DISTANCE estimates (Fig. 3-15).*

This can be explained by Factor 4. Most of the DISTANCE density estimates were lower than the density calculated from group size/forest area. If a group spent a portion of its time outside the forest patch then the DISTANCE estimate would be lower than the group size/forest area estimate. If the group spent most of its time in only a portion of the forest patch the DISTANCE estimate may be much higher. In *Mirador de Naranjo* it appeared that howlers spent most of their time within 1 or 2ha, which explains the high DISTANCE estimate and the low group size/forest area estimate. The smallest home range recorded for howlers is 2ha (Chapman and Balcomb in press).

8. *The large difference between the park's ecological densities and DISTANCE estimates.*

Firstly, density estimates from isolated forest patches will not be similar to estimates from an area within continuous forest (Cant 1978). The current study estimated the densities of monkeys in portions of the highly disturbed and fragmented habitat of the upper plateau of Santa Rosa (Fig. 3-1) which has higher monkey densities than the less fragmented lower plateau (Table 3-6). Many studies have shown a crowding effect of groups within forest patches following forest fragmentation (1040/km^2 in Panama, Baldwin and Baldwin 1976; 77/km^2 in La Pacifica, Clarke et al. 1986; Lovejoy et al. 1986). Furthermore, fragmentation and forest edges result in higher leaf biomass and possibly higher insect biomass (Lovejoy et al. 1986). A density estimate for the entire park would be an average of the upper and lower plateau.

Secondly, the problem with the delimited area method is that it does not account for areas of suitable habitat that are not used (Cant 1978; Fedigan et al. 1985). Density

estimates tend to be higher for study sites where the suitable habitat is clearly defined (e.g. La Pacifica, Clarke et al. 1986).

Lastly, the delimited area method does not recognize 'hot spots' within the park. Chapman (1988) found that 26 capuchins and 40 howlers spent the majority of their time (54-60% of sightings, respectively) in a core area of 13 ha in Santa Rosa. This could result in a density estimate of 108 capuchins/km^2 and 185 howlers/km^2. Chapman (1988) found that the core areas of howler and capuchin home ranges were centered on the oldest forest available. The transects in the current study were not meant to be representative of monkey home ranges, or of the park, but rather of specific forest ages. Chapman's finding suggests that the transects in older forests may have been placed unintentionally within the core areas of monkey home ranges.

9. Density estimates must be interpreted in light of temporal scale.

The density estimate is based on data with equal representation from the dry and rainy season. Therefore, my density estimate is the average of the two seasons. One should realize that the dry season only lasts 4 months of the year, therefore the density estimate from one complete year of sampling will have heavier weight on rainy season data. In the near future the density estimates and habitat preference of the three species will be analyzed separately for each season and the rainy season density estimate could be weighted proportionally to the number of rainy season months in a year.

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